

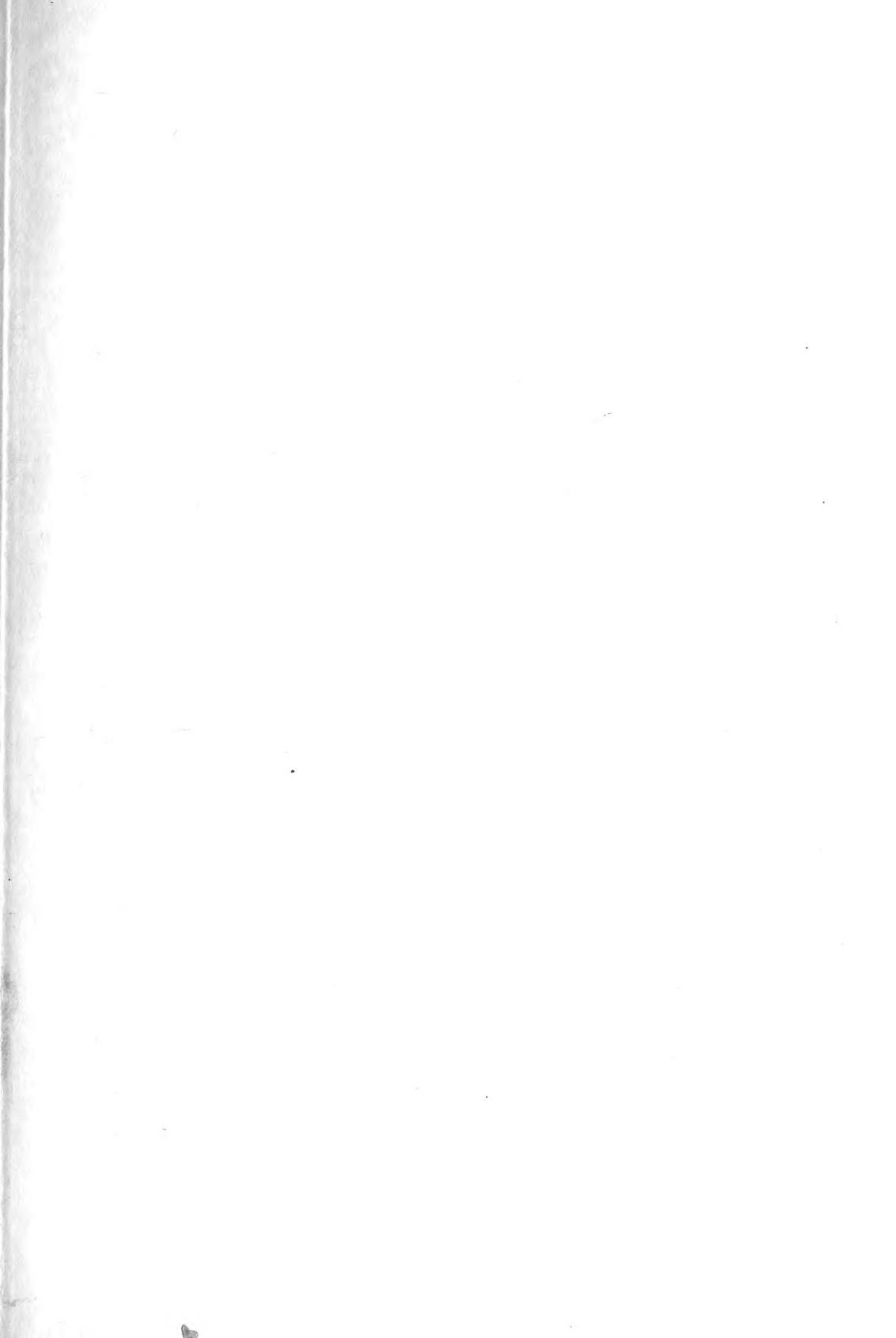


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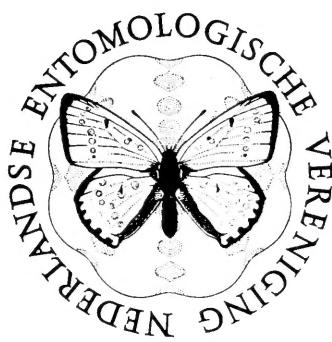
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# TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING



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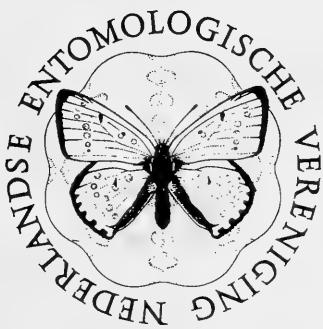
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# REVISIONARY NOTES ON THE GENERA *DAPSILARTHRA* AUCT. AND *MESOCRINA* FOERSTER (HYMENOPTERA, BRACONIDAE, ALYSIINAE)

by

C. VAN ACHTERBERG

Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands

## ABSTRACT

The described species of the genera *Dapsilarthra* auct. and *Mesocrina* Foerster are revised, keyed and partly illustrated. *Dapsilarthra* auct. is divided into two genera, *Adelurola* Strand and *Dapsilarthra* Foerster and a subgeneric division of *Dapsilarthra* is proposed. A neotype is selected for *Mesocrina indagatrix* Foerster, and lectotypes for *Adelura gahani* Baume-Pluvinel, *Alysia apii* Curtis, *A. florimela* Haliday, and *Heterolexis subtilis* Foerster. New combinations are *Prorima thienemanni* (Bischoff), *Adelurola amplidens* (Fischer), *A. florimela* (Haliday), *Dapsilarthra subtilis* (Foerster), *D. indagatrix* (Foerster), *D. dalhouxiensis* (Sharma), and *D. tirolensis* (Königsmann). New synonyms of *Dapsilarthra* are *Heterolexis* Foerster, *Mesocrina* Foerster, *Pseudomesocrina* Königsmann, and *Paraorthostigma* Königsmann. *Opisendea* Foerster is excluded from the synonymy with *Dapsilarthra*. *Opisendea tenuicornis* Foerster, 1862, is a new synonym of *Pentapleura angustata* (Haliday, 1838). *Neocarpa* Fischer is a new junior synonym of *Adelurola* and *Phaenocarpa multiarticulata* Marshall, 1898, is a new junior synonym of *Adelurola florimela* (Haliday, 1838). *Dapsilarthra nowakowskii* Königsmann, 1959, is synonymized with *D. gahani* (Baume-Pluvinel, 1914), *Orthostigma americana* Brues, 1907, with *Dapsilarthra apii* (Curtis, 1826), *Dapsilarthra testacea* Griffiths, 1968, with *Dapsilarthra subtilis* (Foerster, 1862), *Mesocrina venatrix* Marshall, 1895, with *Dapsilarthra indagatrix* (Foerster, 1862), and *Dapsilarthra fuscula* Griffiths, 1968, with *D. rufiventris* (Nees, 1814). Additionally a new species, *Dapsilarthra carpathica* spec. nov., is described from Romania, and a new genus, *Prorima* gen. nov., is erected to include the Oriental species *Mesocrina thienemanni* Bischoff, 1932.

## INTRODUCTION

The capture of a new species of *Dapsilarthra* during my holidays in Romania is the main reason to publish some of the numerous synonomies, which I had already established during my research for a generic revision of the Braconidae. *Adelurola*, previously included in *Dapsilarthra*, stands clearly apart from the rest of the species by virtue of the shape of its mandible and its enlarged 4th antennal segment. The remaining species may be grouped in three subgenera of Foerster, viz., *Heterolexis*, *Mesocrina*, and *Dapsilarthra*. The scanty information on their biology indicates that the groups treated in this paper are endoparasites of mining dipterous larvae, belonging to the families Anthomyiidae, Agromyzidae, Tephritidae, Psilidae, and Scatophagidae.

Species marked with an asterisk are new to the Dutch fauna. For the terminology used in this paper, see Van Achterberg (1979: 242–249).

## KEY TO THE SPECIES OF THE GENERA *Dapsilarthra* AND *Mesocrina* AUCT.

1. Antescutal depression distinct (figs. 95, 96); vein M + CU of hind wing shorter than vein 1-M (fig. 97); claws very slender, sickle-shaped (fig. 101); propodeum completely carinated and antero-dorsal part of propodeum differentiated and about as long as posterior part of propodeum (figs. 95, 99); lower outer orbits of eyes depressed (fig. 98); (genus *Prorima* nov.) ..... *thienemanni* (Bischoff)
- Antescutal depression (virtually) absent (figs. 15, 26, 72); vein M + CU of hind wing longer than vein 1-M (figs. 6, 70); claws less slender (figs. 10, 22, 32, 47); propodeum not carinated; antero-dorsal part of propodeum not differentiated (fig. 1) or much shorter than posterior part (fig. 26); lower outer orbits of eyes flat or convex (fig. 12) ..... 2
2. Mandible with a ventral (4th) lamelliform

- protuberance (figs. 12, 13, 42); 4th antennal segment longer than 3rd segment or subequal (figs. 1, 2); pterostigma wide and elliptical (figs. 6, 14, 40); vein  $r$  of fore wing emerging (sub)medially from pterostigma (fig. 6); precoxal sulcus sculptured (fig. 1); (genus *Adelurola* Strand) ..... 3
- Mandible without ventral lamelliform protuberance (figs. 19, 27, 29, 46); 4th antennal segment shorter than 3rd segment (fig. 43), or subequal (fig. 72); pterostigma, vein  $r$  of fore wing and precoxal sulcus variable; (genus *Dapsilarthra* Foerster) ..... 5
3. Vein 1-R1 (metacarp) of fore wing almost straight; marginal cell of fore wing comparatively short (fig. 40) ..... *amplidens* (Fischer)
- Vein 1-R1 of fore wing distinctly curved; marginal cell of fore wing comparatively long (fig. 6) ..... 4
4. Head distinctly transverse; dorsal length of eye 0.8—1.1 times dorsal length of temple (fig. 9) ..... *florimela* (Haliday)
- Head (sub)cubical; dorsal length of eye 0.6—0.7 times dorsal length of temple ..... *asiatica* Telenga
5. Vein CU1b and apical half of vein 2-1A of fore wing absent, resulting in an open 1st subdiscal cell; vein CU1a of fore wing at same level as vein 2-CU1 (fig. 17); vein m-cu of fore wing antefurcal (fig. 17) or subinterstitial; (subgenus *Heterolexis* Foerster) ..... 6
- Vein CU1b and apical half of vein 2-1A of fore wing present, resulting in a closed 1st subdiscal cell (figs. 29, 58); vein CU1a of fore wing situated below level of vein 2-CU1 (figs. 58, 80); vein m-cu of fore wing variable ..... 10
6. Middle lobe of mesoscutum evenly setose; medial groove of mesoscutum more or less developed posteriorly; antennal segments 45—52; parasite of Tephritidae ..... *dictynna* (Marshall)
- Middle lobe of mesoscutum largely glabrous; medial groove of mesoscutum absent (fig. 24); antennal segments 25—48; parasites of Agromyzidae ..... 7
7. Scutellar sulcus smooth (fig. 24); notaular absent; precoxal sulcus crenulate (fig. 15); antennal segments 25—29 ..... *gahani* (Baume-Pluvine)
- Scutellar sulcus more or less crenulate; notaular and precoxal sulcus variable; antennal segments 27—48 ..... 8
8. Eyes rather converging below, the maximum width of head 2.2—2.7 times the minimum width of face; antennal segments 27—33; precoxal sulcus smooth; notaular not impressed in disk of mesoscutum; 1st tergite dark and strongly contrasting with yellowish 2nd tergite ..... *levisulca* Griffiths
- Eyes scarcely converging below, the maximum width of head 1.8—2.1 times the minimum width of face; antennal segments 31—48, if 33 or less then 1st tergite not distinctly contrasting with 2nd tergite; precoxal sulcus usually sculptured; notaular variable ..... 9
9. The anteriorly impressed part of notaular longer, reaching the disk of mesoscutum; antennal segments 34—48; 1st metasomal tergite dark brown or black, distinctly contrasting with middle of 2nd tergite ..... *balteata* (Thomson)
- Notaular short, not or slightly impressed in disk of mesoscutum; antennal segments 31—33; 1st metasomal tergite yellowish or reddish, not distinctly contrasting with middle of 2nd tergite ..... *subtilis* (Foerster)
10. Vein 3-CU1 of fore wing longer than vein CU1b (figs. 28, 35, 51); pterostigma largely elliptical; vein  $r$  emerging submedially from elliptical part of pterostigma (figs. 28, 45); vein m-cu of hind wing present (figs. 28, 45); metasoma of ♀ of type-species strongly compressed, of ♂ depressed; vein m-cu of fore wing shortly postfurcal (fig. 45); (subgenus *Mesocrina* Foerster) ..... 11
- Vein 3-CU1 of fore wing shorter than vein CU1b (figs. 57, 58, 80) or equal (fig. 89); pterostigma (sub)linear, with its sides (sub)parallel (figs. 58, 82); vein  $r$  emerging between base and middle of pterostigma (figs. 70, 82); vein m-cu of hind wing absent (fig. 70); metasoma of both sexes largely depressed; vein m-cu of fore wing variable (subgenus *Dapsilarthra* Foerster) ..... 12
11. Precoxal sulcus present (fig. 31); posterior part of propodeum subvertical, steep, and distinctly differentiated from antero-dorsal part of propodeum (fig. 26); dorsope comparatively small (fig. 37); sides of 1st tergite diverging apically ..... *dalbouiensis* (Sharma)
- Precoxal sulcus absent (fig. 43); posterior part of propodeum continuous with antero-dorsal part, slightly oblique (fig. 43); dorsope large (fig. 50); sides of 1st tergite sub-

- parallel ..... *indagatrix* (Foerster)
12. Vein  $r$  of fore wing (very) short, shorter than width of pterostigma (figs. 82, 90) or subequal (fig. 38); pterostigma not reaching beyond middle of marginal cell of fore wing, rather stout (figs. 38, 82, 90); vein  $m$ -cu of fore wing shortly antefurcal (fig. 38) ..... 13
- Vein  $r$  of fore wing comparatively long, longer than width of pterostigma (figs. 58, 70); pterostigma reaching beyond middle of marginal cell of fore wing, and slender (figs. 58, 70); vein  $m$ -cu of fore wing shortly postfurcal (fig. 70) or subinterstitial ..... 15
13. Antennal segments 40—41; vein 3-CU1 of fore wing subhorizontal (fig. 89); antenna about twice as long as body ..... *isabella* (Haliday)
- Antennal segments 25—33; vein 3-CU1 of fore wing oblique or subvertical (figs. 38, 92); antenna shorter than twice length of body ..... 14
14. Antenna short, about 1.3 times length of body; marginal cell of fore wing distinctly removed from wing apex (fig. 38); hind femur and tibia dark brown ..... *tirolensis* (Königsmann)
- Antenna medium-sized, about 1.7 times length of body; marginal cell of fore wing comparatively close to wing apex (fig. 90); hind femur and tibia brownish-yellow; (nominate form has hind coxa and 2nd tergite yellowish, which are largely dark brown or blackish in forma *fuscula* Griffiths) ..... *rufiventris* (Nees)
15. Notauli distinctly impressed posteriorly; precoxal sulcus extensively sculptured ..... *sylvia* (Haliday)
- Posterior half of notauli absent (fig. 78); precoxal sulcus smooth or narrowly and superficially sculptured (figs. 56, 72) ..... 16
16. Sides of mandible parallel (figs. 61, 62); laterope absent (fig. 56); 3rd and 4th antennal segments yellowish; vein 1-R1 (metacarp) of fore wing less curved (fig. 58); ventral half of side of pronotum largely smooth (fig. 56); length of fore wing ca. 2.8 mm ..... *carpathica* spec. nov.
- Mandible widened dorsally (figs. 68, 69), because of the protruding 1st tooth; laterope present (fig. 72); 3rd and 4th antennal segments dark brown; vein 1-R1 of fore wing more curved (fig. 70); ventral half of side of pronotum distinctly sculptured

(fig. 72); length of fore wing 3.5—4.8 mm ..... *apii* (Curtis)

### Genus *Prorima* nov.

Type-species: *Mesocrina thienemanni* Bischoff, 1932.

**Etymology:** From “pro” (Latin for “in front of”, “forward”) and “rima” (Latin for “cleft”) because of the antescutal depression on the anterior part of the mesosoma.

**Diagnosis.** — Fourth antennal segment slightly shorter than 3rd segment (including annulus); eyes glabrous, not emarginate (fig. 104); lower outer orbits of eyes depressed (fig. 98); mandible slender, parallelsided, with 3 small teeth, 2nd tooth somewhat longer than 1st tooth, without ventral protruding tooth or lamella, and with carina to 3rd tooth (fig. 98); antescutal depression distinct (figs. 95, 96); pronope medium-sized (fig. 99); medio-posterior groove of mesoscutum present (fig. 99); precoxal sulcus present, superficially crenulate (fig. 95); metanotum blunt dorsally (fig. 95); propodeum completely areolated (fig. 99), its anterodorsal part differentiated and about as long as posterior part of propodeum (fig. 95); pterostigma elliptical; vein  $r$  emerges somewhat behind middle of pterostigma (fig. 97); vein CU1b of fore wing present, somewhat longer than vein 3-CU1 (fig. 105); 1st subdiscal cell of fore wing closed; vein  $m$ -cu of fore wing distinctly postfurcal (fig. 97); vein  $M + CU$  of hind wing shorter than vein 1-M (fig. 97); vein  $m$ -cu of hind wing faintly indicated; marginal cell of hind wing medium-sized (fig. 97); claws very slender, sickle-shaped (fig. 101); dorsope large (fig. 102); 2nd tergite smooth; ovipositor sheath (fig. 106) longer than apical height of metasoma.

**Distribution.** — Contains only the Oriental type-species.

#### *Prorima thienemanni* (Bischoff) comb. nov. (figs. 95—108)

*Mesocrina thienemanni* Bischoff, 1932: 742—744, fig. 5. Shenefelt, 1974: 996.

**Holotype,** ♀, length of head and mesosoma combined 1.5 mm, of fore wing 2.8 mm.

**Head.** — Antenna missing, except for scapus and pedicellus; an earlier examination proved that the length of the 3rd segment is slightly longer than 4th segment; length of maxillary palp about 0.7 times height of head; dorsal length of eye 2.0 times temple (fig. 103); POL:

$\varnothing$  ocellus : OOL = 5 : 3 : 9; frons flat, smooth; vertex smooth, with deep medio-longitudinal suture (fig. 103); face smooth, rather flat; anterior tentorial pits medium-sized, far removed from eyes (fig. 104); clypeus rather convex, smooth, its apical margin not differentiated; length of malar space 0.3 times basal width of mandible; medial length of mandible 1.3 times its basal width.

Mesosoma. — Length of mesosoma 1.8 times its height; side of pronotum smooth, except for the transverse crenulate groove (fig. 95); pre-coxal sulcus narrowly impressed, superficially crenulate anteriorly, but posteriorly absent (fig. 95); pleural suture smooth dorsally, narrowly crenulate ventrally; episternal scrobe large, deep, connected to pleural suture (fig. 95); metapleural flange absent; metapleuron largely smooth, but ventrally rugose; only anterior third of notauli impressed and crenulate, rest absent; medial suture long, reaching midpoint of mesoscutum (fig. 99); mesoscutum largely glabrous; scutellar sulcus wide, deep, without distinct longitudinal carinae; scutellum completely smooth, rather flat; metanotum with medial carina anteriorly; medial carina of propodeum long (fig. 99); posterior part of propodeum with a narrow areola; propodeal spiracle small, round and far from anterior margin of propodeum (fig. 95).

Wings. — Fore wing: vein 1-SR rather long (fig. 97); r : 3-SR : SR1 = 4 : 19 : 32; 1-SR + M slightly sinuate; SR1 straight; cu-a short, postfurcal; 1-CU1 : 2-CU1 = 3 : 31; 1st subdiscal cell about 5 times its maximum width (fig. 105); basal half of M + CU1 not or indistinctly sclerotized; 2-SR : 3-SR : r-m = 12 : 19 : 6; m-cu strongly converging to 1-M (fig. 97). Hind wing: cu-a short, rather reclivous; M + CU : 1-M = 10 : 12; marginal cell absent apically.

Legs. — Hind coxa smooth; only claws of middle leg present, long setose, with minute lobe (fig. 101); length of femur and tibia of hind leg 5.2 and 8.6 times their width, respectively; 3rd and 4th tarsal segments of middle leg subquadrate (fig. 101).

Metasoma. — Length of 1st tergite 1.7 times its apical width, its surface largely smooth, but between dorsal carinae rugose (fig. 102), basally concave, rest strongly convex; dorsal carinae of 1st tergite present in basal  $\frac{1}{4}$  of tergite; spiracles of 1st tergite just in front of middle of tergite, protruding (fig. 102); glymma wide anteriorly; laterope rather small, shallow (fig. 95); dorsope deep, diameter of dorsope equal to

about half their distance apart (fig. 102); ovipositor slender; length of ovipositor sheath 0.46 times fore wing; hypopygium sharp apically, large (fig. 108).

Colour. — Dark brown; legs, scapus, pedicellus, palpi, tegulae, and metasoma ventrally, yellowish; pterostigma brown; wing membrane slightly infuscated.

Holotype in Zoologisches Museum, Berlin: "West-Java, Tjibodas, 14.7.29, Thienemann S.", "*Mesocrina thienemanni* Bisch., Typ., det Bischoff", "Typus", "Präp. 18.2.55/ 1 ♀". Metasoma largely on separate slide.

Notes. — In existing keys this species runs to *Pseudomesocrina* Königsmann (= *Mesocrina* Foerster), however, it certainly does not belong in this genus. In particular the long vein 1-M of hind wing, the depression of the lower outer orbits, the long vein CU1b of fore wing, the long anterodorsal part of the propodeum, the presence of the antescutal depression and the shape of the claws indicate that this species is more closely related to *Phaenocarpa*. However, *M. thienemanni* differs from *Phaenocarpa* by the postfurcal vein m-cu of fore wing, the short 4th antennal segment (but some spp. of *Phaenocarpa* have similar antennae), the presence of an antescutal depression, and of a depression at the lower outer orbits of the eyes (the latter is sometimes shallowly indicated in *Phaenocarpa*), preventing its inclusion in *Phaenocarpa*. The new genus also differs from *Dinotrema*, mainly by the wide pterostigma, the antescutal depression, the large claws, and the antero-dorsal part of the propodeum being subequal to its posterior or part.

#### Genus *Adelurola* Strand stat. nov.

*Adelura* Foerster, 1862: 267 (nec Bonaparte, 1854).  
Shenefelt, 1974: 986.

*Adelurola* Strand, 1928: 51 (nom. nov. for *Adelura* Foerster). Shenefelt, 1974: 986—987.

*Neocarpa* Fischer, 1966: 185. Shenefelt, 1974: 987.  
Syn. nov.

Type-species: *Alysia florimela* Haliday, 1838.

Diagnosis. — Fourth antennal segment longer than 3rd segment (figs. 1, 2) or subequal; apical antennal segment without spine; lower outer orbits flat or convex (fig. 12); eyes glabrous, not emarginate; mandible strongly widened dorsally, with a ventral (4th) lamelliform protuberance (figs. 12, 42); pronope small and shallow or absent (fig. 4); antescutal depression absent; medio-posterior groove of mesoscutum present (fig. 4); precoxal sulcus sculp-

tured (fig. 1); metanotum blunt dorsally (fig. 1); antero-dorsal part of propodeum not differentiated from posterior part of propodeum (fig. 1); pterostigma wide and largely elliptical (figs. 6, 14); vein M + CU1 of fore wing largely unsclerotized; vein r of fore wing emerging (sub)medially from pterostigma (fig. 6); vein CU1b of fore wing present, longer than vein 3-CU1 (fig. 8); 1st subdiscal cell of fore wing closed; vein m-cu of fore wing slightly postfurcal (figs. 6, 14); vein M + CU of hind wing longer than vein 1-M (fig. 6); vein m-cu of hind wing absent; marginal cell of hind wing medium-sized basally (fig. 6); claws moderately slender (fig. 10), not sickle-shaped; dorsope large (fig. 7); 2nd tergite smooth; setae of metasoma in subapical rows; ovipositor sheath shorter than apical height of metasoma (fig. 1).

**Distribution.** — Contains 3 Palaearctic species.

**Adelurola amplidens** (Fischer) comb. nov.  
(figs. 40—42)

*Neocarpa amplidens* Fischer, 1966: 185, figs. 9—11.  
*Dapsilarthra amplidens*; Shenefelt, 1974: 987.

Only known from 4 ♂ from Iraq, of which the holotype should be housed in the Zoologische Sammlung des Bayerischen Staates in München, where it could not be traced. Owing to the kindness of Dr. Fischer I was able to examine two topotypic paratypes upon which the insertion in the key is based. This species is very close to *A. florimela*; the difference of the short marginal cell of fore wing is not significant because this is also common in males of *florimela* (fig. 14).

**Adelurola florimela** (Haliday) comb. nov.  
(figs. 1—14)

*Alysia florimela* Haliday, 1838: 239.  
*Dapsilarthra florimela*; Shenefelt, 1974: 988—989.

*Phaenocarpa multiarticulata* Marshall, 1898: 245.

**Syn. nov.**

*Dapsilarthra multiarticulata*; Shenefelt, 1974: 989.

*Dapsilarthra pentapleuroides* Fischer, 1971: 85, figs. 25—27 (unavailable name, used in synonymy with *D. multiarticulata*).

Redescribed after a female from the Netherlands (Linschoterbos), compared with the lectotype, length of body 3.3 mm, of fore wing 3.7 mm.

**Head.** — Antennal segments 43, long setose, length of 3rd segment 0.9 times 4th segment (fig. 2), length of 3rd and 4th segments 3.4 and

3.6 times their width, respectively; penultimate segment of antenna 2.6 times its width (fig. 5), and apical segment without spine; length of maxillary palp 1.1 times height of head; dorsal length of eye 1.1 times temple; POL : Ø ocellus: OOL = 5 : 3 : 12; frons slightly convex, medially somewhat rugose, laterally partly punctulate, rest smooth (fig. 9); vertex smooth, with medial groove; face medially convex, somewhat punctulate and microsculptured, shiny; anterior tentorial pits large, far removed from eyes (fig. 3); clypeus strongly convex, punctate; apical margin of clypeus straight, narrow, thin and differentiated; malar space almost absent (fig. 12); 2nd tooth of mandible longer and sharper than both lateral, more lobe-shaped teeth (fig. 13).

**Mesosoma.** — Length of mesosoma 1.5 times its height; side of pronotum rugose ventrally, rest smooth; epicnemial area rugose; precoxal sulcus only medially developed (fig. 2), deep, rugose; rest of mesopleuron smooth; pleural sulcus crenulate ventrally, almost smooth dorsally (fig. 1); episternal scrobe deep, elliptical; metapleural flange absent; metapleuron largely coarsely reticulate-rugose; notaui only anteriorly impressed, microsculptured, rest absent; mesoscutal lobes glabrous medially; medial groove of mesoscutum rather long (fig. 4); scutellar sulcus deep, with one longitudinal carina; scutellum punctulate; metanotum with rather long medial carina (fig. 4); surface of propodeum coarsely reticulate-rugose, no medial carina or areola; propodeal spiracle small, round, submedially.

**Wings.** — Fore wing: 1-SR rather long (fig. 6); r : 3-SR : SR1 = 4 : 18 : 42; 1-SR + M and SR1 slightly curved; cu-a medium-sized, postfurcal; 1-CU1 : 2-CU1 = 9 : 25; 2-SR : 3-SR : r-m = 13 : 18 : 7; m-cu parallel to 1-M (fig. 6). Hind wing: cu-a rather short (fig. 6); marginal cell narrowed apically.

**Legs.** — Hind coxa smooth; tarsal claws slender, setose (fig. 10); length of femur, tibia, and basitarsus of hind leg 4.1, 9.5, and 7.0 times their width, respectively; length of hind tibial spurs 0.3 and 0.4 times hind basitarsus.

**Metasoma.** — Length of 1st tergite 1.8 times its apical width, its surface behind the spiracles coarsely rugose (fig. 7), medio-basally concave, rest convex; dorsal carinae of 1st tergite present almost to apex of tergite, united at about mid-segment (fig. 7); glymma rather wide, without laterope (fig. 1); dorsope deep, large, their diameter about equal to their distance apart;

ovipositor straight; length of ovipositor sheath 0.06 times fore wing; hypopygium large (fig. 1), truncate apically.

Colour. — Black; scapus, annellus, palpi, veins of hind wing mainly, tegulae, and legs, light yellowish; mandibles, antenna (except for scapus and annellus), pterostigma, most of fore wing veins, and metasoma behind 1st tergite, dark brown; apical  $\frac{2}{3}$  of hind tibia and base of hind tarsus darkened.

Redescribed after a specimen in the Rijksmuseum van Natuurlijke Historie, Leiden: "Linschoterbos, 8.x.1966, v. Ooststroom", "compared & conspecific with lectotype of *Alysia florimela* Haliday, C. v. Achterberg, 1979". The type-series in the Haliday Collection (Dublin) consists of 1 ♀ and 1 ♂, both with the label "British Haliday, 20.2.82/Box 10 AWS." Originally I was inclined to consider only the ♀ an original type-specimen, because Haliday did not state he had a male. However, Stelfox in a copy of his notes (discovered by Dr. C. O'Riordan and a partial copy kindly supplied by Dr. J. P. O'Connor) stated under *Alysia florimela* Haliday, that Haliday did include the male: "In describing the male of this species as unknown Marshall (Trans. ent. Soc. London, 1895, p. 365) fell into error. When describing species of which he had only one sex Haliday always began his diagnosis with the words *mas* or *fem.* as the case might be: — e.g., "Sp. 43. Punctigera. Al. & c. fem. *fusco-castanea* . . ." or again "Sp. 48. *Perdita* Al & c. *mas nigra* . . ."

On the other hand, when he had both sexes before him, he only mentioned the sexes when referring to some character which belonged to that sex alone: in the present case "*fem. terebra subexerta*" and "*fem. corpore duplo longiores articulus 50.*" That he had both sexes of the present species is manifest, for box 10 I found a ♂ & a ♀ beside each other (on 26.1.1935)."

The indirect evidence put forward by Stelfox in his notes makes it possible to accept both specimens from box 10 as types; I prefer to designate here the ♀ as lectotype (and not the ♂ as Stelfox did without publishing it). The ♀ lectotype is in a fairly good condition, the antenna has 50 segments (as stated by Haliday) and the dorsal length of the eye is 1.1 times the dorsal length of the temple. The lectotype stems from England (London). In the Haliday Collection there are two specimens (1 ♀ ("Clifden, July 8, [18]39") and 1 ♂, which do not belong to the type series. Additionally 9 ♀ and 5 ♂ were examined from the Netherlands (Waarder; Aspe-

ren; Udenhout), West Germany (Taufkirchen bei München), and Bulgaria (Rhodopi Mountains, Thagortsharn; id., N. Zdraves). The specimen from Den Haag reported by Snellen van Vollenhoven (1873: 195) belongs to *Phaenocarpa*.

Variation. — Antennal segments 43—54; length of 3rd segment 0.9—1.0 times 4th segment; dorsal length of eye 0.8—1.1 times dorsal length of temple; vein 2-SR of one fore wing of specimen from N. Zdraves partly absent; pterostigma of male enlarged (fig. 14); metasoma of some specimens more or less yellowish banded.

Note. — The proposed synonymy is based on the redescription by Fischer (1971) and the variation found in the series collected in the Netherlands. *A. florimela* is an easily recognizable species, with is not uncommon in Waarder (Netherlands). The enlargement of the pterostigma in the male misled Marshall, so that he described the male as a separate species (*multiarticulata*). *A. florimela* has been reared from *Pegomya nigratarsis* Zetterstedt (Anthomyiidae) and *Acidia cognata* (Wiedemann) (Tephritidae).

#### *Adelurola asiatica* Telenga

*Adelurola asiatica* Telenga, 1935: 186.

*Dapsilarthra asiatica*; Shenefelt, 1974: 987.

The type from Turkestan (USSR) is destroyed and additional specimens of this species have not been recorded.

#### Genus *Dapsilarthra* Foerster

*Gnaptodon* Haliday, 1833: 265 (suppression requested to ICZN).

*Dapsilarthra* Foerster, 1862: 267. Shenefelt, 1974: 986—991. Marsh, 1979: 222.

*Heterolexis* Foerster, 1862: 268; Shenefelt, 1974: 992.

##### Syn. nov.

*Grammospila* Foerster, 1862: 269; Shenefelt, 1974: 987.

*Mesocrina* Foerster, 1862: 266; Shenefelt, 1974: 996.

##### Syn. nov.

*Pseudomesocrina* Königsmann, 1959b: 611; Shenefelt, 1974: 1018. *Syn. nov.*

*Paraorthostigma* Königsmann, 1972: 25—26, 1 fig. *Syn. nov.*

Diagnosis. — Antennal segments 25—52; 4th antennal segment shorter than 3rd segment (fig. 43) or subequal (fig. 72); apical segment of antenna without spine; eyes glabrous, not emarginate; lower outer orbits of eyes flat or convex (fig. 29); mandible without ventral lamelliform protuberance (figs. 29, 46), robust (fig. 29) or

slender (fig. 25); pronope usually absent (fig. 49), seldom present (fig. 24); antescutal depression absent; medio-posterior groove of mesoscutum present (fig. 49) or absent (fig. 24); metanotum blunt dorsally (fig. 15) or slightly protruding (fig. 26); propodeum not carinated, its antero-dorsal part not differentiated from posterior part (fig. 72) or much shorter than posterior part (fig. 26); vein 1-SR of fore wing medium-sized (fig. 58), exceptionally short (fig. 28); 1st subdiscal cell of fore wing parallel-sided; vein M + CU1 of fore wing largely unsclerotized; vein M + CU of hind wing longer than vein 1-M; marginal cell of hind wing narrowed apically or subparallel; claws moderately slender, not sickle-shaped (figs. 22, 32); dorsope rather small (fig. 18) to large (fig. 50); laterope absent or shallow; 2nd tergite smooth; setae of metasoma in subapical rows; length of ovipositor sheath subequal to apical depth of metasoma (fig. 54) or shorter (fig. 72).

**Distribution.** — All three subgenera occur in the Palaearctic region (including the Himalayan area), the subgenus *Dapsilarthra* Foerster also occurs in the Nearctic region (partly introduced).

#### Subgenus *Heterolexis* Foerster stat. nov.

*Heterolexis* Foerster, 1862: 268. Shenefelt, 1974: 992.  
*Grammospila* Foerster, 1862: 269. Shenefelt, 1974:  
987. **Syn. nov.**

**Diagnosis.** — Antennal segments 25—52; medio-posterior groove of mesoscutum absent (fig. 24), only present in *dictynna*; precoxal sulcus impressed, smooth or crenulate (fig. 15); vein CU1b and apical half of vein 2-1A of fore wing absent, resulting in an open 1st subdiscal cell (fig. 17); vein CU1a of fore wing at same level as vein 2-CU1; vein r of fore wing arising before middle of pterostigma; vein m-cu of fore wing antefurcal (fig. 17) or subintersital; pterostigma linear (fig. 17); dorsope rather small (fig. 18).

**Distribution.** — Contains five Palaearctic species; one species is introduced in North America (Hendrickson & Barth, 1979).

#### *Dapsilarthra (Heterolexis) dictynna* (Marshall)

*Adelura dictynna* Marshall, 1895a: 422—423, fig. 6.  
*Dapsilarthra dictynna*; Königsmann, 1972: 22. Shenefelt, 1974: 988.

A scarcely collected but widespread species; not yet collected in the Netherlands. Examined:

1 ♀ (Bulgaria, Rhodopi Mountains, Pamporova) and 1 ♂ (Switzerland, Aeschi-Ried, 1000 m). Parasite of *Pycnoglossa flavipennis* (Fallén) (Tephritidae) in *Pteridium aquilinum* L.

#### *Dapsilarthra (Heterolexis) gahani* (Baume-Pluvinel)

(figs. 15—25)

*Adelura gahani* Baume-Pluvinel, 1915: 47, 11 figs.

*Dapsilarthra gahani*; Shenefelt, 1974: 989.

*Dapsilarthra nowakowskii* Königsmann, 1959a: 591, figs. Shenefelt, 1974: 989. **Syn. nov.**

**Lectotype**, ♀, length of body 1.5 mm, of fore wing 2.1 mm.

**Head.** — Antennal segments 29, length of 3rd segment 1.1 times 4th segment, length of 3rd and 4th segments 4.5 and 4.0 times their width, respectively; penultimate segment of antenna 3.0 times its width (fig. 20); length of maxillary palp 0.6 times height of head; dorsal length of eye 1.3 times temple (fig. 21); POL : Ø ocellus : OOL = 14 : 5 : 18; frons flat and smooth; vertex smooth, with medial groove; face slightly convex, smooth; anterior tentorial pits very large, wider than long and almost reaching eyes (fig. 16); clypeus convex and smooth, its ventral margin not differentiated, straight medially; eye nearly touching base of mandible (fig. 15); mandible rather slender, not widened apically (fig. 25), with three sharp teeth.

**Mesosoma.** — Length of mesosoma 0.9 times its height; pronope distinct (fig. 24); pronotal side largely smooth, except for some rugae (fig. 15); precoxal sulcus rather shallow and rugulose; rest of mesopleuron smooth; pleural sulcus finely crenulate; episternal scrobe narrow (fig. 15); metapleural flange absent; metapleuron largely smooth; notailli absent on dorsal disc of mesoscutum (fig. 24), faintly impressed in front of disc (fig. 15); mesoscutum rather convex, largely glabrous and smooth; medio-posterior groove of mesoscutum absent; scutellar sulcus deep, with no carinae (fig. 24); scutellum rather flat and smooth; surface of propodeum largely smooth, except for some rugosity, without medial carina or areola; posterior pat of propodeum not differentiated from antero-dorsal part; propodeal spiracle small and in front of middle of propodeum.

**Wings.** — Fore wing: r : 3-SR : SR1 = 8 : 24 : 92; SR1 sinuate (fig. 17); 1-CU1 : 2-CU1 = 3 : 14; 2-SR : 3-SR : r-m = 18 : 24 : 11. Hindwing: cu-a reclivous; marginal cell (sub)parallel-sided apically.

Legs. — Hind coxa smooth; tarsal claws minute, slender (fig. 22); length of femur, tibia and basitarsus of hind leg 5.2, 7.8, and 4.5 times their width, respectively; inner hind spur about  $\frac{1}{4}$  times hind basitarsus, outer spur not visible (at 80 X).

Metasoma. — Length of 1st tergite 2.0 times its apical width, its surface rugulose, medially convex, basally and latero-posteriorly flat (fig. 18); dorsal carinae of 1st tergite present in basal half of 1st tergite; laterope absent; length of ovipositor sheath 0.05 times fore wing, somewhat widened medially and upcurved (fig. 15); hypopygium large, truncate apically.

Colour. — Dark brown (blackish according to the original description); base of 2nd tergite yellowish-brown; scapus and pedicellus ventrally, 3rd and 4th antennal segments, mandibles, palpi, and legs, yellowish; wings hyaline; pterostigma light brown.

Lectotype in U.S. National Museum, Washington: "Ex *Phytomyza* sp. on Columbine", "Lucerne, Switzerland", "G. de Baume-Pluvineill Col.", "PHO 14, La Baume. 3 Rd'Ulm Paris", "Adulura gahani B.-P., det. Gahan Cestest(?)". Basis of original identification by A.B.G." This ♀ is here designated as lectotype. One paralectotype, ♀, topotypic, in same collection; it has the ovipositor sheath retracted, not protruding; antennal segments 29; length of fore wing 2.2 mm, of body 1.2 mm.

Note. — Parasite of *Phytomyza minuscula* Goureau and *P. aquilegiae* Hardy (Agromyzidae); recorded from Poland and Switzerland.

**Dapsilarthra (Heterolexis) levisulca** Griffiths  
*Dapsilarthra levisulca* Griffiths, 1968a: 10. Shenefelt, 1974: 989.

Only known from the type-series from Yugoslavia, partly reared from *Phytomyza bellidina* Hering (Agromyzidae).

\* **Dapsilarthra (Heterolexis) balteata**  
(Thomson)

*Alysia balteata* Thomson, 1895: 2288.

*Dapsilarthra balteata*; Königsmann, 1972: 21. Shenefelt, 1974: 988. Hendrickson & Barth, 1979: 168, 170.

This common species has been reared from many leaf-mining species, belonging to the genera *Agromyza*, *Cerodonta*, *Phytomyza*, and *Liriomyza* (Agromyzidae). The record from *Pegomya* (Anthomyiidae) needs to be confirm-

ed. Specimens examined: 91 ♀ and 3 ♂ from the Netherlands (Waarder, Driebergen, Wijster, Lienden, Ouddorp, Weesp, Kadier en Keer). Variation: antennal segments 39–48; precoxal sulcus smooth or slightly sculptured; 1st tergite black, dark brown or brownish; head behind eyes parallel-sided to strongly widened posteriorly; 2nd and 3rd tergites of metasoma frequently medially brownish-yellow, but colour of metasoma behind 1st tergite varies from largely piceous and dark brown to light yellowish and brown.

\* **Dapsilarthra (Heterolexis) subtilis** (Foerster)  
comb. nov.

*Heterolexis subtilis* Foerster, 1862: 268. Shenefelt, 1974: 992.

*Dapsilarthra testacea* Griffiths, 1968a: 9–10; Königsmann, 1972: 22. Shenefelt, 1974: 991. **Syn. nov.**

In the Foerster Collection (Zoologisches Museum, Berlin) there are two males on one pin ("25/212", "Aachen, Juni", "Frst", "*subtilis* Frst"), of which the ♂ nearest to the pin is here designated as lectotype. Both are typical specimens of *Dapsilarthra testacea*. The 1st and 2nd segments of the metasoma are yellowish; the lectotype has 31, and the paralectotype 32 antennal segments.

This species is seldom collected; reported from Germany and Austria. In the Leiden collection are specimens from the Netherlands (Ede and Putten).

Subgenus **Mesocrina** Foerster stat. nov.

*Mesocrina* Foerster, 1862: 266. Shenefelt, 1974: 996.  
*Pseudomesocrina* Königsmann, 1959b: 611. Shenefelt, 1974: 1018. **Syn. nov.**

Diagnosis. — Antennal segments about 38 (only known for type-species); medio-posterior groove of mesoscutum present (fig. 49); precoxal sulcus absent (fig. 43) or impressed (fig. 26); vein CU1b and apical half of vein 2-1A of fore wing present, resulting in a closed 1st subdiscal cell (fig. 28); vein 3-CU1 of fore wing longer than vein CU1b (fig. 51); pterostigma largely elliptical (figs. 28, 45); vein r of fore wing emerging submedially from elliptical part of pterostigma; vein m-cu of hind wing present (fig. 28); vein m-cu of fore wing shortly postfurcal (fig. 45); dorsope small (fig. 37) or large (fig. 50).

Distribution. — Contains one West Palaearctic species and one species from the Himalayan area.

**\* Dapsilarthra (Mesocrina) indagatrix**

(Foerster) comb. nov.

(figs. 43—55)

*Mesocrina indagatrix* Foerster, 1862: 266. Shenefelt, 1974: 996.*Mesocrina venatrix* Marshall, 1895a: 429—430, fig. Shenefelt, 1974: 1018—1019. *Syn. nov.*

The interpretation of this obviously scarcely collected species has been hindered by the loss of the type (Königsmann, 1959b: 611), but in my opinion the fairly complete original description by Foerster enables a correct identification of the species to be made. This interpretation is close to that of Marshall (1895a: 430) and disagrees with the statements made by Königsmann (1959b: 610). Königsmann's argument that Foerster was unlikely to have overlooked the strongly compressed metasoma of the ♀ is not conclusive, because Foerster's specimen may have been a ♂, which has a normally depressed metasoma. Because no closely related species are known, there is no reason to doubt the synonymy of *venatrix* and *indagatrix*. The holotype of *D. venatrix* (Marshall) has been examined; it is a ♀ with the typical compressed metasoma. To fix the type-species of the genus *Mesocrina* Foerster I designate here the ♂ described and figured below as neotype of *Mesocrina indagatrix* Foerster, 1862.

**Neotype, ♂**, length of body 3.5 mm, of fore wing 3.9 mm.

**Head.** — Antennal segments 21 (apical segments missing), length of 3rd segment 1.7 times 4th segment, length of 3rd and 4th segments 4.5 and 2.4 times their width, respectively; penultimate segment of antenna of neotype missing, but in ♀ from Ede (Netherlands), length 1.7 times its width (fig. 55); length of maxillary palp 1.2 times height of head; dorsal length of eye subequal to dorsal length of temple (fig. 53); POL : Ø ocellus : OOL = 12 : 7 : 20; frons smooth, vertex smooth and with medial suture; face rather flat and with some punctulation (fig. 44); anterior tentorial pits large and far removed from eyes, distance to eyes 1.5 times maximal diameter of pit; clypeus strongly convex, smooth, its apical margin narrowly differentiated and straight medially; malar space short, eye almost touching base of mandible (fig. 46); mandible slightly widened dorsally, 2nd tooth sharp and longer than both lateral, more obtuse teeth (figs. 46, 48).

**Mesosoma.** — Length of mesosoma 1.4 times its height; pronope absent (fig. 49); side of pro-

notum with a crenulate medial groove, rest smooth (fig. 43); precoxal sulcus absent; mesopleuron smooth; pleural sulcus narrowly crenulate ventrally, dorsally largely smooth (fig. 43); metapleural flange absent; metapleuron smooth, but crenulate rugose-reticulate; notaui only anteriorly impressed and crenulate (fig. 49); mesoscutum largely glabrous, only anteriorly densely setose; medio-posterior groove long and narrow, rather shallow (fig. 49); scutellar sulcus with one weak longitudinal carina; scutellum sparsely punctulate; side of scutellum smooth; surface of propodeum anteriorly and medio-posteriorly finely rugulose, rest mainly smooth, medial carina and areola absent; posterior part of propodeum not differentiated from antero-dorsal part; propodeal spiracle rather small, round, somewhat protruding and in front of middle of propodeum.

**Wings.** — Fore wing: r much shorter than width of pterostigma (fig. 45); r : 3-SR : SR1 = 3 : 21 : 41; SR1 straight; 1-CU1 : 2-CU1 = 6 : 17; 2-SR : 3-SR : r-m = 17 : 21 : 9; 1st subdiscal cell somewhat widened apically. Hind wing: cu-a straight; marginal cell absent apically.

**Legs.** — Hind coxa punctulate; tarsal claws rather slender (fig. 47); length of femur, tibia and basitarsus of hind leg 4.8, 8.2, and 6.2 times their width, respectively; length of hind tibial spurs 0.3 and 0.4 times hind basitarsus.

**Metasoma.** — Length of 1st tergite 2.0 times its apical width, its surface basally smooth, its posterior half rugose (fig. 50), basally concave, medially convex; dorsal carina of 1st tergite present in basal 0.9 of tergite, but apically superficial; dorsope large (fig. 50); hypopygium of neotype rather short, truncate apically; ♀ from Ede has length of ovipositor sheath 0.13 times fore wing, ovipositor slender, with no distinct teeth or nodus, only slightly widened subapically (fig. 54); hypopygium medium-sized and subtruncate apically; metasoma of neotype ♂ depressed (fig. 43), of ♀ strongly compressed (fig. 54).

**Colour.** — Black; metasoma behind 1st tergite, wing veins, and tegulae, brownish-yellow; hind tarsus and apex of hind tibia somewhat infuscated; wing membrane subhyaline.

**Neotype** in the Zoologische Staatssammlung, München: "Harthausen b. München, A. 27.9.68, Haeselb.". Additional specimens examined: 1 ♀, Museum Budapest, holotype of *Mesocrina venatrix* Marshall ("venatrix M., Coll. Marshall", "*Pseudomesocrina venatrix*

(Marsh), det. Königsmann") from England, which is conspecific with the neotype of *indagatrix*. Length of fore wing 3.7 mm, and length of ovipositors sheath about 0.12 times fore wing. First metasomal tergite missing (figured by Königsmann), rest of metasoma on separate slide, and antenna incomplete. 1 ♀, Rijksmuseum van Natuurlijke Historie, Leiden: Netherlands ("Ede, trap [= Malaise-trap], 22—28.ix, Van Rossem"). Length of fore wing 4.2 mm, of body 4.3 mm; metanotum rather coarsely sculptured; length of 1st tergite 1.9 times its apical width. Parasite of *Pegomya* and *Amaurosoma* spp. (Anthomyiidae and Scatophagidae, respectively).

**Dapsilarthra (Mesocrina) dalhousiensis**  
(Sharma) comb. nov.  
(figs. 26—37)

*Acrobela dalhousiensis* Sharma, 1978: 127—128, figs. 4—6.

Holotype, ♂, length of body 5.4 mm, of fore wing 4.7 mm.

**Head.** — Remaining antennal segments 11, apical segments missing, scapus compressed; length of 3rd segment 1.2 times 4th segment, length of 3rd and 4th segments 3.0 and 2.6 times their width, respectively; length of maxillary palp 1.2 times height of head; dorsal length of eye 1.2 times temple; temple smooth and subparallel-sided (fig. 31); POL : Ø ocellus : OOL = 8 : 4 : 14; frons flat and smooth; vertex with medial groove; face unevenly convex, largely smooth, with some punctulation (fig. 30); anterior tentorial pits large, far removed from eyes (fig. 30); clypeus convex, somewhat punctulate, rugulose near dorsal margin, its apical margin not distinctly differentiated medially, convex; malar space absent, eye touching base of mandible (fig. 27); mandible widened dorso-apically, finely rugose medially, 3rd tooth large and lobe-shaped; ventral margin of mandible with small incision (fig. 29) (but without ventral protruding lamella); 2nd tooth of mandible large, longer than lateral teeth, acute apically (figs. 27, 29).

**Mesosoma.** — Length of mesosoma 1.2 times its height; pronope absent; side of pronotum medially crenulate, dorsally largely smooth, ventrally microsculptured (fig. 26); epicnemial area ventrally rugose (fig. 26); precoxal sulcus present in anterior 0.7 of mesopleuron, densely reticulate-rugose; rest of mesopleuron smooth; pleural sulcus rather shallow and narrow, finely crenulate (fig. 26); episternal scrobe large;

metapleural flange small, obtuse apically; metapleuron finely rugose; notaui only anteriorly impressed, finely crenulate (fig. 34); mesoscutal lobes smooth, medially glabrous; medio-posterior groove of mesoscutum slender, also anteriorly with a shallow groove (fig. 34); scutellar sulcus deep, long, with 8 longitudinal carinae; scutellum smooth; sides of scutellum rugose; metanotum somewhat protruding medially (fig. 26); posterior part of propodeum differentiated and much longer than antero-dorsal part (fig. 26); surface of propodeum densely rugose anteriorly, with some short apical carinae and indistinct sculpture posteriorly, medial carina and areola absent; propodeal spiracle rather small, round, and in front of middle of propodeum.

**Wings.** — Fore wing: r subequal to width of pterostigma (fig. 28); r : 3-SR : SR1 = 8 : 28 : 61; SR1 straight; 1-CU1 : 2-CU1 = 2 : 20; 2-SR : 3-SR : r-m = 18 : 28 : 13; 3-SR of left wing with stub (fig. 36), indistinct in right wing (fig. 28). Hind wing: cu-a straight; marginal cell narrowed apically.

**Legs.** — Hind coxa smooth; tarsal claws rather slender (fig. 32); length of femur, tibia and basitarsus of hind leg 3.9, 8.9, and 6.4 times their width, respectively; length of hind tibial spurs 0.3 times hind basitarsus, subequal.

**Metasoma.** — Length of 1st tergite equal to its apical width, its surface largely striate (fig. 37), flat basally, and medially slightly convex; dorsal carinae distinct in front of spiracles, short (fig. 37); dorsope small; metasoma depressed; hypopygium medium-sized and truncate apically.

**Colour.** — Black; mesonotum, pronotum (largely), mesosternum and mandible, brownish-red; legs (except for middle and hind tarsi, apex of hind tibia and femur), palpi, tegulae, scapus, and pedicellus, yellowish; pterostigma, most wing veins, metasoma (dorsally rather blackish), fore and middle tarsi (except telotarsi), apices of hind femur and tibia partly, dark brown; wing membrane slightly infuscate.

Holotype (and only known specimen) in Gupta Collection, Delhi: "India: H.P. Dalhousie, 2132 m, 22.ix.1971, Sykh. Dev. No. JD 158", "Holotype *Acrobela dalhousiensis* V. Sharma, 1975". Biology unknown.

**Subgenus Dapsilarthra** Foerster  
*Dapsilarthra* Foerster, 1862: 267. Shenefelt, 1974: 986—991. Marsh, 1979: 222.  
*Paraorthostigma* Königsmann, 1972: 25—26, 1 fig.  
Syn. nov.

**Diagnosis.** — Antennal segments 25—41: medio-posterior groove of mesoscutum present (fig. 67); precoxal sulcus present (fig. 81) or almost absent (fig. 72); vein CU1b and apical half of vein 2-1A of fore wing present, resulting in a closed 1st subdiscal cell (fig. 58); vein 3-CU1 of fore wing shorter than vein CU1b (fig. 57) or equal (fig. 89); pterostigma (sub)linear, with its sides (sub)parallel (figs. 58, 82); vein  $r$  of fore wing emerging between base and middle of pterostigma (fig. 70, 82); vein  $m-cu$  of hind wing absent (fig. 70); dorsope (rather) large (figs. 66, 79, 91).

**Distribution.** — Five Palaearctic species, two of which also occur in the Nearctic region.

**Dapsilarthra (Dapsilarthra) rufiventris (Nees)**  
(figs. 90, 92)

*Bassus rufiventris* Nees, 1814: 213.

*Dapsilarthra rufiventris*; Königsmann, 1972: 22.  
Shenefelt, 1974: 989—990. Marsh, 1979: 222.

*Alysia flaviventris* Haliday, 1838: 240.

*Dapsilarthra flaviventris*; Shenefelt, 1974: 990.

*Alysia gracilicornis* Thomson, 1895: 2283. Shenefelt, 1974: 990.

*Phaenocarpa ochrogaster* Szépligeti, 1898: 393, 406.  
Shenefelt, 1974: 1012.

*Dapsilarthra fuscula* Griffiths, 1968b: 65—66. Shenefelt, 1974: 989. **Syn. nov.**

Because the differences between *rufiventris* and *fuscula* seem to be completely restricted to differences in colour and I have examined intermediately coloured specimens from Romania and Bulgaria, I consider *fuscula* to be only a melanistic form of *rufiventris*. Total specimens examined; 20 ♀ and 5 ♂ (nominate form) and 3 ♀ of f. *fuscula* Griffiths, all in the Rijksmuseum van Natuurlijke Historie, Leiden, except for the Bulgarian specimens from the Zaykov Collection, Plovdiv. The specimens originate from the Netherlands (Waarder, Breukelen, Thorn (ex *Trilobomyza flavifrons* Meigen in *Melandrium rubrum* Garcke), Lienden (ex ? *Napomyza glechomae* Kaltenbach in *Glechoma hederacea* L.), Wijster), Switzerland (Schwyz, Brunnen), Romania (Sinaia, S. Carpathians, 1300–1400 m), and Bulgaria (Pamporovo, Rhodopi Mountains (f. *fuscula*); Velinograd, Rhodopi Mountains (nominate form)). Parasite of *Liriomyza*, *Phytomyza*, and *Trilobomyza* spp. (Agromyzidae) in herbaceous plants.

**Dapsilarthra (Dapsilarthra) isabella (Haliday)**  
(figs. 81—89, 93, 94)

*Alysia isabella* Haliday, 1838: 240.

*Dapsilarthra isabella*; Shenefelt, 1974: 989.

Redescribed from a ♀ in the Marshall Collection from Barnstaple, England. Precise length of body unknown, because part of the metasoma has been removed; length of fore wing 3.1 mm.

**Head.** — Antenna about twice length of body, with 41 segments (fig. 81), length of 3rd segment 1.2 times 4th segment, length of 3rd and 4th segments 3.7 and 3.0 times their width, respectively; length of penultimate antennal segment 2.5 times its width (fig. 83); length of maxillary palp equal to height of head; dorsal length of eye equal to dorsal length of temple (fig. 87); temples subparallel-sided; POL : Ø ocellus: OOL = 4 : 3 : 10; frons flat and smooth; vertex smooth, without medial groove; face rather convex, laterally coriaceous (fig. 85); anterior tentorial pits large, far removed from eyes (fig. 85); clypeus convex and smooth, its apical margin straight medially and with a narrow rim; malar space almost absent; mandible smooth, slightly widened apically (figs. 84, 88), its middle tooth acute, somewhat longer than lateral, more lobe-shaped teeth.

**Mesosoma.** — Length of mesosoma 1.3 times its height; pronope absent; side of pronotum smooth, except for a crenulate medial groove (fig. 81); epicnemial area largely crenulate; precoxal sulcus only medially distinctly impressed and crenulate (fig. 81); rest of mesopleuron smooth; pleural sulcus finely crenulate; episternal scrobe medium-sized; metapleural flange medium-sized, rather acute apically; metapleuron largely smooth (only ventrally somewhat rugose), and with a pit close to the mesopleuron (fig. 81); notauli only anteriorly impressed and finely crenulate, but absent on dorsal part of mesoscutum (figs. 81, 94); mesoscutum largely glabrous, smooth; medio-posterior pit of mesoscutum elliptical and rather deep (fig. 94); scutellar sulcus deep, finely crenulate; scutellum smooth; side of scutellum smooth; metanotum posteriorly rather bluntly protruding (fig. 81); surface of propodeum densely and finely rugose; medial carina and areola of propodeum absent; posterior part of propodeum not differentiated from antero-dorsal part; propodeal spiracle round, rather small and protruding, in front of middle of propodeum.

**Wings.** — Fore wing:  $r$  very short, shorter than width of pterostigma (fig. 82); pterostigma not reaching beyond middle of marginal cell and rather wide (fig. 82);  $m-cu$  shortly antefurcal; 3-CU1 subhorizontal (fig. 89); marginal cell almost attaining wing apex;  $r$  : 3-SR : SR1 = 2 : 26 : 58; SR1 sinuate; 1-CU1 : 2-CU1 =

1 : 11; CU1b subvertical and equal to 3-CU1 (fig. 89); 2-SR : 3-SR : r-m = 12 : 26 : 6. Hind wing: cu-a straight; marginal cell absent apically.

Legs. — Hind coxa smooth; tarsal claws slender (fig. 86); length of femur, tibia and basitarsus of hind leg 4.7, 9.2, and 4.7 times their width, respectively; length of hind tibial spurs 0.3 times hind basitarsus, subequal.

Metasoma. — Length of 1st tergite 1.6 times its apical width, its surface coarsely punctate-rugose (fig. 91), antero-medially concave, and medially convex; dorsal carina of 1st tergite absent; distance between dorsope far more than their width (fig. 91); ovipositor missing, but according to Marshall (1895b: 366) subexserted.

Colour. — Black or blackish-brown; antenna dark brown, but basally partly yellowish; palpi, legs (except for the infuscated apical half of hind tibia and base of hind coxae), and tegulae, brownish-yellow; wing membrane hyaline; pterostigma, wing veins, and 2nd tergite, brown.

Type-series (obviously consisting of one male received from Walker, from the surroundings of London) could not be found in the Haliday Collection (Dublin) and is probably lost. The redescription is based on the ♀ in the Marshall Collection (British Museum, London): "England, ND, Barnstaple, Marshall Coll., B.M. 1904—120", "*Isabella* Hal.", "In B.M. 1950, Under *Adelura isabella* Hal.", "prep. 20.3.59/1".

*Alysia isabella* Haliday has not been recognized since Marshall (1895a, 1895b). Because the redescribed ♀ fully agrees with Haliday's fairly complete description and Marshall is the first revisor, Marshall's interpretation has to be accepted. The biology is unknown.

#### Dapsilarthra (Dapsilarthra) sylvia (Haliday)

*Alysia sylvia* Haliday, 1839: 25.

*Dapsilarthra sylvia*; Königsmann, 1972: 22. Shenefelt, 1974: 990—991.

This is a sparsely collected species, not yet found in the Netherlands. Parasite of *Agromyza*, *Cerodontha*, *Phytomyza*, and *Trilobomyza* spp. (Agromyzidae) in herbaceous plants.

#### Dapsilarthra (Dapsilarthra) tirolensis

(Königsmann) comb. nov.

*Paraorthostigma tirolense* Königsmann, 1972: 26, fig.

Owing to the kindness of Dr. E. Haeselbarth (München) I was able to examine the holotype of *Paraorthostigma tirolense* (♂, Haeselbarth Collection: "Unser Frau in Schnals, Südtirol, 1600 m, 14.7.66, Hbth", "Holotypus", "*Paraorthostigma tirolense* n.sp"). It belongs to the subgenus *Dapsilarthra*, is close to *rufiventris*, and differs mainly by the dark legs, somewhat longer vein r (fig. 38), short antenna (fig. 39) and shorter marginal cell of fore wing (fig. 38 versus fig. 90).

#### Dapsilarthra (Dapsilarthra) carpathica spec. nov.

(figs. 56—67)

Holotype, ♀, length of body 1.8 mm, of fore wing 2.8 mm.

Head. — Antennal segments 34 (but apical segments missing), length of 3rd segment 1.1 times 4th segment, length of 3rd and 4th segments 4.7 and 4.2 times their width, respectively; scapus rather slender (fig. 65); length of maxillary palp 1.1 times height of head; dorsal length of eye 1.6 times temple; temple roundly narrowed posteriorly (fig. 63); POL : Ø ocellus : OOL = 7 : 4 : 12; frons smooth, with small medial pit; vertex smooth, with shallow groove (fig. 63); face smooth, rather flat; anterior tentorial pits large, less robust than in *apii*, oval, not well differentiated from face, distance to eye about 1/3 of maximum diameter of pit (fig. 59); clypeus convex and smooth, its apical margin slightly differentiated and convex medially (fig. 59); malar space absent; sides of mandible parallel, rather slender (figs. 61, 62), 2nd tooth acute, longer than both, more lobe-shaped lateral teeth, without distinct carinae.

Mesosoma. — Length of mesosoma 1.2 times its height; pronope absent; side of pronotum largely smooth, only medially crenulate (fig. 56); precoxal sulcus rather slender, superficially sculptured, anteriorly and posteriorly absent (fig. 56); rest of mesopleuron smooth; pleural sulcus dorsally largely smooth, ventrally finely crenulate (fig. 56); episternal scrobe slender; metapleural flange medium-sized, directed forwards; metapleuron ventrally rugulose, dorsally largely smooth; notaui anteriorly impressed and crenulate (fig. 67), but posterior half absent; mesoscutum largely smooth and glabrous; medio-posterior groove of mesoscutum medium-sized, deep; scutellar suture with one longitudinal carina; scutellum (including sides) smooth; metanotum posteriorly coriaceous and medial

carina short (fig. 67); surface of propodeum reticulate-rugulose; medial carina and areola of propodeum absent; posterior part of propodeum not differentiated from antero-dorsal part; propodeal spiracle rather small, round, in front of middle of propodeum.

**Wings.** — Fore wing: r longer than width of pterostigma (fig. 58); pterostigma reaching beyond middle of marginal cell and slender; m-cu shortly postfurcal (fig. 58); 3-CU1 oblique and shorter than CU1b (fig. 57); 1-R1 less curved than in *apii* (fig. 58 versus fig. 70); r : 3-SR : SR1 = 13 : 49 : 119; SR1 almost straight; 1-CU1 : 2-CU1 = 7 : 22; 2-SR : 3-SR : r-m = 17 : 49 : 16. Hind wing; cu-a almost straight; marginal cell parallel-sided apically.

**Legs.** — Hind coxa smooth; tarsal claws rather slender (fig. 64); length of femur, tibia, and basitarsus of hind leg 6.4, 10.4 and 6.3 times hind basitarsus, respectively.

**Metasoma.** — Length of 1st tergite 2.2 times its apical width, its surface rugulose, flat medio-basally, rest convex; dorsal carinae of 1st tergite present in front of spiracles; laterope absent; dorsope medium-sized (fig. 66); ovipositor straight, its apex somewhat curved downwards, without notch or nodus, with some ventral teeth; length of ovipositor sheath 0.07 times fore wing, sheath somewhat widened subapically; hypopygium large, truncate apically (fig. 56).

**Colour.** — Black; tegulae basally dark brown, apically yellowish; palpi whitish; face, antenna (except 4 basal segments) and metasoma behind 1st tergite, dark brown; wing veins, and pterostigma, brown; mandibles, labrum, legs, and 4 basal segments of antenna, largely yellowish; apex of hind tibia and telotarsi somewhat infuscated; wing membrane hyaline.

Holotype (and only known specimen) in the Rijksmuseum van Natuurlijke Historie, Leiden: "Museum Leiden, Romania, Sinaia, S. Carpathians, 1300—1400 m, 8—10.viii.1978, C. van Achterberg".

#### *Dapsilarthra* (*Dapsilarthra*) *apii* (Curtis) (figs. 68—80)

*Alysia apii* Curtis, 1826: 141, figs.

*Dapsilarthra apii*; Shenefelt, 1974: 987.

*Alysia laevipectus* Thomson, 1895: 2288.

*Orthostigma americana* Brues, 1907: 59—60. **Syn. nov.**

*Dapsilarthra americana*; Fischer, 1973: 256—258, fig. 8.

Redescribed after a female from Austria (Aschbach, Tirol), which is compared and conspecific with the lectotype of *Alysia apii* Curtis; length of body 3.6 mm, of fore wing 4.8 mm.

**Head.** — Antennal segments 50, 3rd segment equal to 4th segment, length of 3rd and 4th segments both 4.0 times their width; scapus very robust, compressed (fig. 75); penultimate segment of antenna 3.3 times its width (fig. 71); length of maxillary palp 1.3 times height of head; dorsal length of eye 1.2 times temple (fig. 73); temples subparallel-sided, rounded posteriorly; POL : Ø ocellus; OOL = 6 : 3 : 12; frons smooth, except for a shallow medial impression (fig. 74); vertex smooth, with medial groove: face rather flat, largely shiny-coriaceous; anterior tentorial pits large, not well differentiated from face, distance to eye about equal to maximum diameter of pit (fig. 74); clypeus convex, punctulate, its apical margin superficially differentiated, weakly convex (fig. 74); malar space absent; mandible robust, widened apically (figs. 68, 69), with 2nd tooth large and acute, longer than both large and more lobe-shaped lateral teeth.

**Mesosoma.** — Length of mesosoma 1.2 times its height; pronope absent, except for a narrow slit-shaped depression (fig. 78); side of pronotum dorsally smooth, its ventral half largely rugose (fig. 72); epicnemial area ventrally crenulate, dorsally smooth; only anterior half of pre-coxal sulcus impressed, smooth (fig. 72); rest of mesopleuron smooth; pleural sulcus very finely crenulate; episternal scrobe linear (fig. 72); metapleural flange medium-sized, directed forwards; metapleuron rugulose, but medially smooth; notaui anteriorly impressed (fig. 78), their posterior half absent; between notaui two rows of punctures, rest of mesoscutal lobes smooth; medio-posterior groove medium-sized, droplet-shaped (fig. 78); scutellar sulcus finely crenulate (but in lectotype of *apii* and in specimen from Sölden with one medial carina only); scutellum and its sides smooth; metanotum with weak superficial crest (fig. 78), slightly protruding dorsally (fig. 72); surface of propodeum densely rugulose, with no carina; posterior part of propodeum not differentiated from antero-dorsal part (fig. 72), with a scarcely differentiated oval areola; propodeal spiracle rather small, round and in front of middle of propodeum.

**Wings.** — r longer than width of pterostigma (fig. 70); pterostigma reaching beyond middle

of marginal cell, and slender; m-cu shortly postfurcal; marginal cell ends close to wing apex (fig. 70); 1-R1 strongly curved; r : 3-SR : SR1 = 6 : 25 : 58; SR1 curved; 1-CU1 : 2-CU1 = 9 : 36; CU1b longer than 3-CU1; 3-CU1 oblique (fig. 80); 2-SR : 3-SR : r-m = 10 : 25 : 8. Hind wing: cu-a reclivous; marginal cell parallel-sided apically.

Legs. — Hind coxa smooth; tarsal claws rather slender (fig. 76); length of femur, tibia, and basitarsus of hind leg 5.6, 10.8, and 6.2 times their width, respectively.

Metasoma. — Length of 1st tergite 1.7 times its apical width, its surface rugulose, flat mediobasally, medially convex; dorsal carinae present in basal third, in front of spiracles (fig. 79); laterope deep and large (fig. 72); dorsope large, their distance apart much more than diameter of dorsope (fig. 79); ovipositor straight; ovipositor sheath 0.05 times fore wing, long setose (fig. 72); hypopygium large, truncate apically.

Colour. — Black; antenna, 2nd tergite, clypeus, hind tibia and tarsus largely, wing veins (largely), and tegulae, dark brown; pterostigma brown; palpi, labrum, and rest of legs, yellowish; wing membrane subhyaline.

Redescribed ♀ in the Rijksmuseum van Natuurlijke Historie, Leiden: "Austria, Tirol, Aschbach, 1400 m, 16.viii.1975, C. J. Zwakhals".

Lectotype of *Alysia apii* Curtis, 1826, here designated: ♀, Curtis Collection (Melbourne): "30", "apii", "Type", "Type of *Alysia apii* Curt., G. Nixon det. 1948" [unpublished]. The figure of *apii* given in the original description is fairly correct, but the separately figured wing (fig. 9) obviously belongs to another species (vein 3-SR shorter than 2-SR!). Curtis had more than one specimen, because he used the pleural form ("For specimens of this insect and their history I am indebted to a lady . . ."); the only remaining specimen has to be accepted as lectotype.

The holotype of *Orthostigma americana* Brues (Milwaukee Public Museum, Milwaukee) is a female of rather small size and with whitish palpi, not, however, essentially differing from *apii*. It bears the following labels: "Milw., Co. Wis., vi-18, 1906", "Type", "*Orthostigma americana* Brues", "22062". Additionally examined 1 ♀ (Rijksmuseum van Natuurlijke Historie, Leiden). "Austria, Tirol, Sölden, 1800 m, 17.viii.1975, C. J. Zwakhals". It has vein SR1 of the fore wing less curved, while the palpi, scapus, pedicellus, and hind tibia (except apex) are

more reddish than of the figured specimen. The specimen reported from Driebergen by Snellen van Vollenhoven (1873: 195) belongs to *D. balteata* (Thomson).

Parasite of *Philipphylla heraclei* L. (Tephritidae) and *Psila rosae* F. (Psilidae).

#### Species excluded from *Dapsilarthra*

##### *Dapsilartha tenuicornis* (Foerster)

*Opisenda tenuicornis* Foerster, 1862: 266.

*Dapsilartha tenuicornis*; Shenefelt, 1974: 991.

*Pentapleura angustula* Haliday, 1838: 229 Syn. nov.

The lectotype (♀, Zoologisches Museum, Berlin) of *O. tenuicornis* has the ventral protuberance of the mandible comparatively weakly developed, and vein 3-SR of fore wing is somewhat longer than vein 2-SR; however, both features are not uncommon among *Pentapleura* spp.

##### *Dapsilarthra sulcifera* Papp

*Dapsilarthra sulcifera* Papp, 1967: 209, figs. Shenefelt, 1974: 990.

*Opius comatus* Wesmael, 1835; Fischer, 1974: 48.

As pointed out by Fischer (1974) this species was wrongly assigned to the Alysiinae.

##### *Dapsilarthra barthii* (Brues)

*Asobara barthii* Brues, 1907: 57—58.

*Dapsilarthra barthii*; Fischer, 1973: 258—260, figs. 9—10.

I have examined the lectotype selected by Fischer (♀, Milwaukee Public Museum, Milwaukee); it proved to be a *Phaenocarpa* species with stout antenna (however, 3rd antennal segment distinctly shorter than 4th segment). *Phaenocarpa barthii* (Brues, 1907) is a new combination, except for the (accidental?) use of this combination in the text to figs. 9—10 in Fischer, 1973.

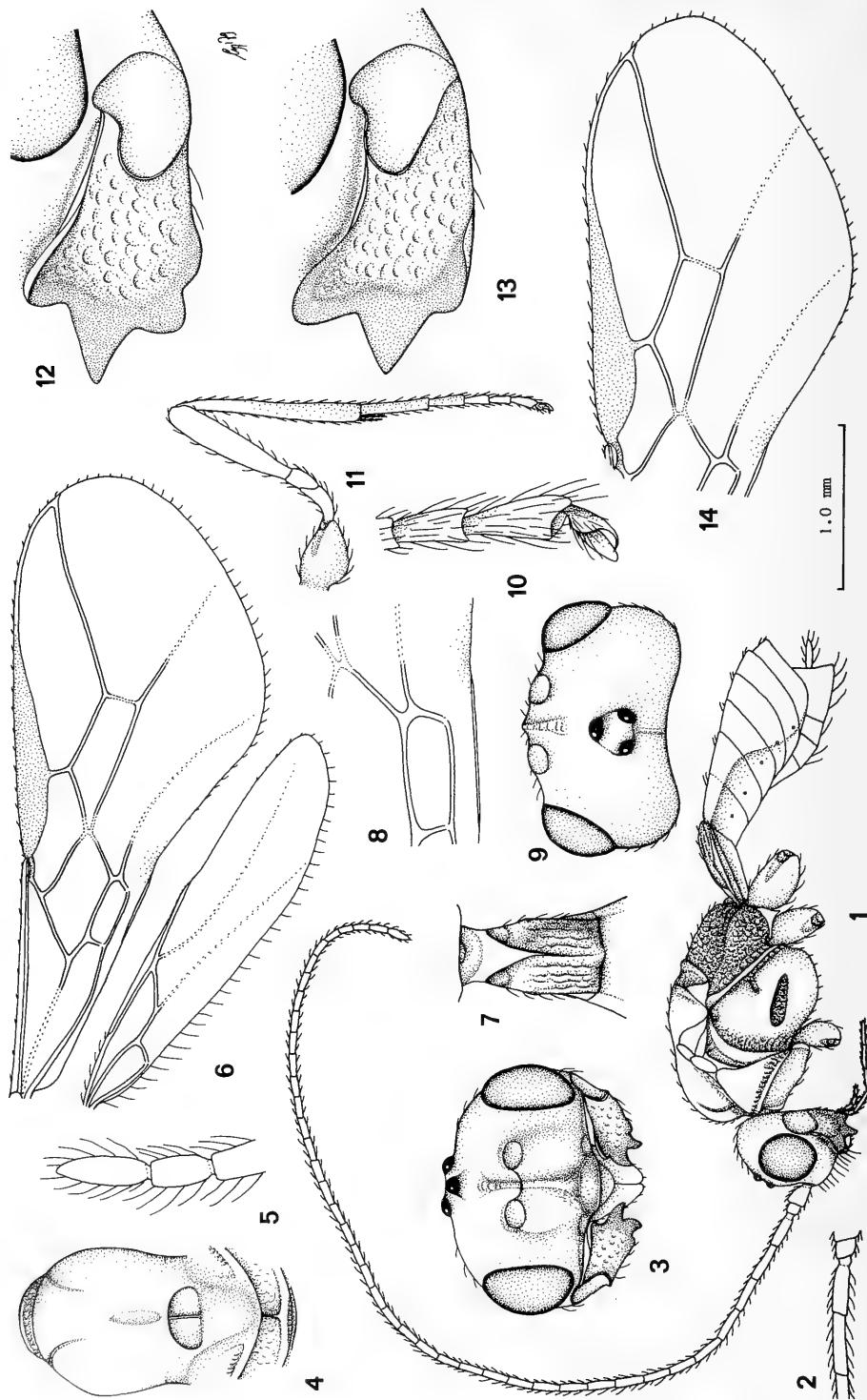
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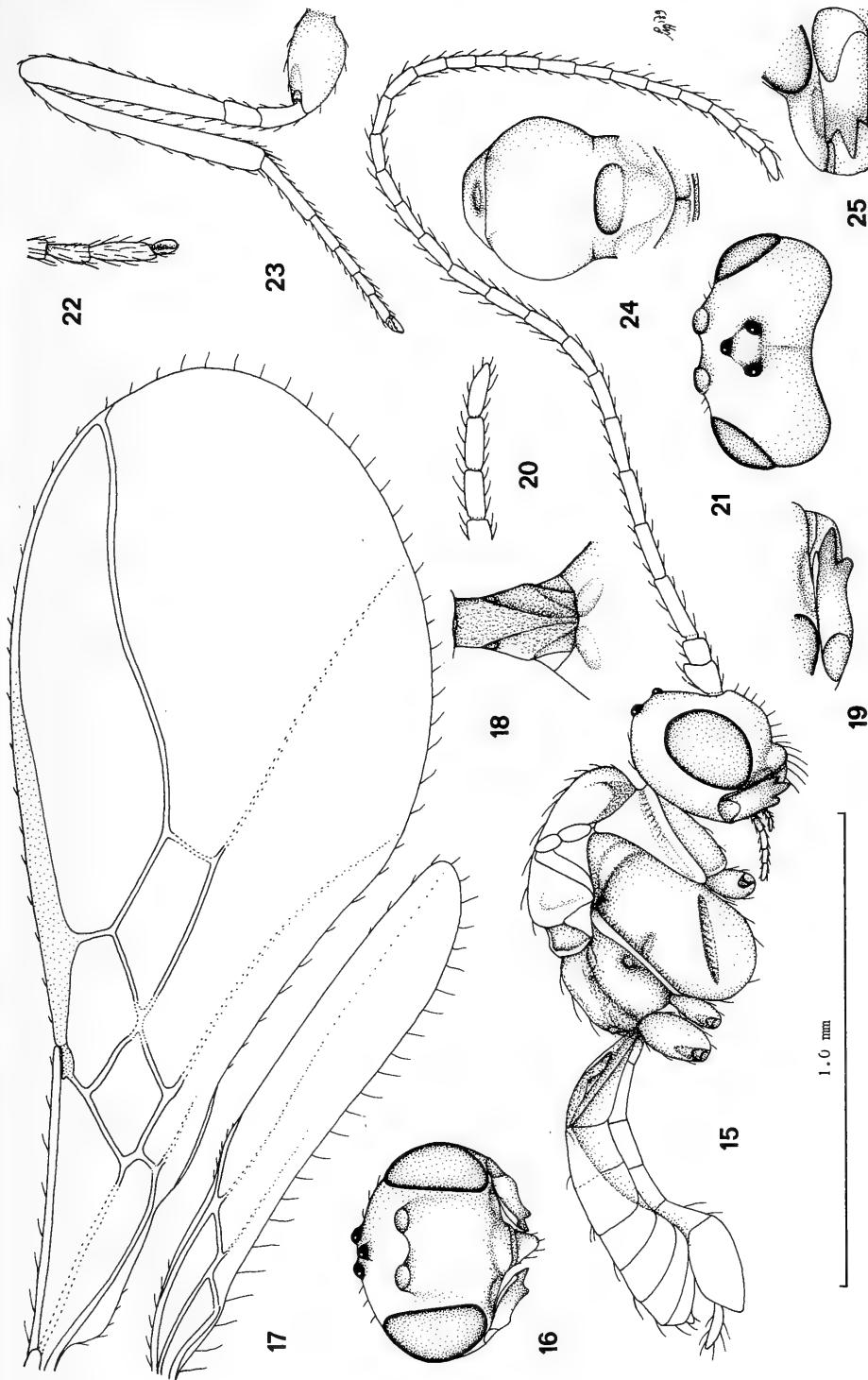
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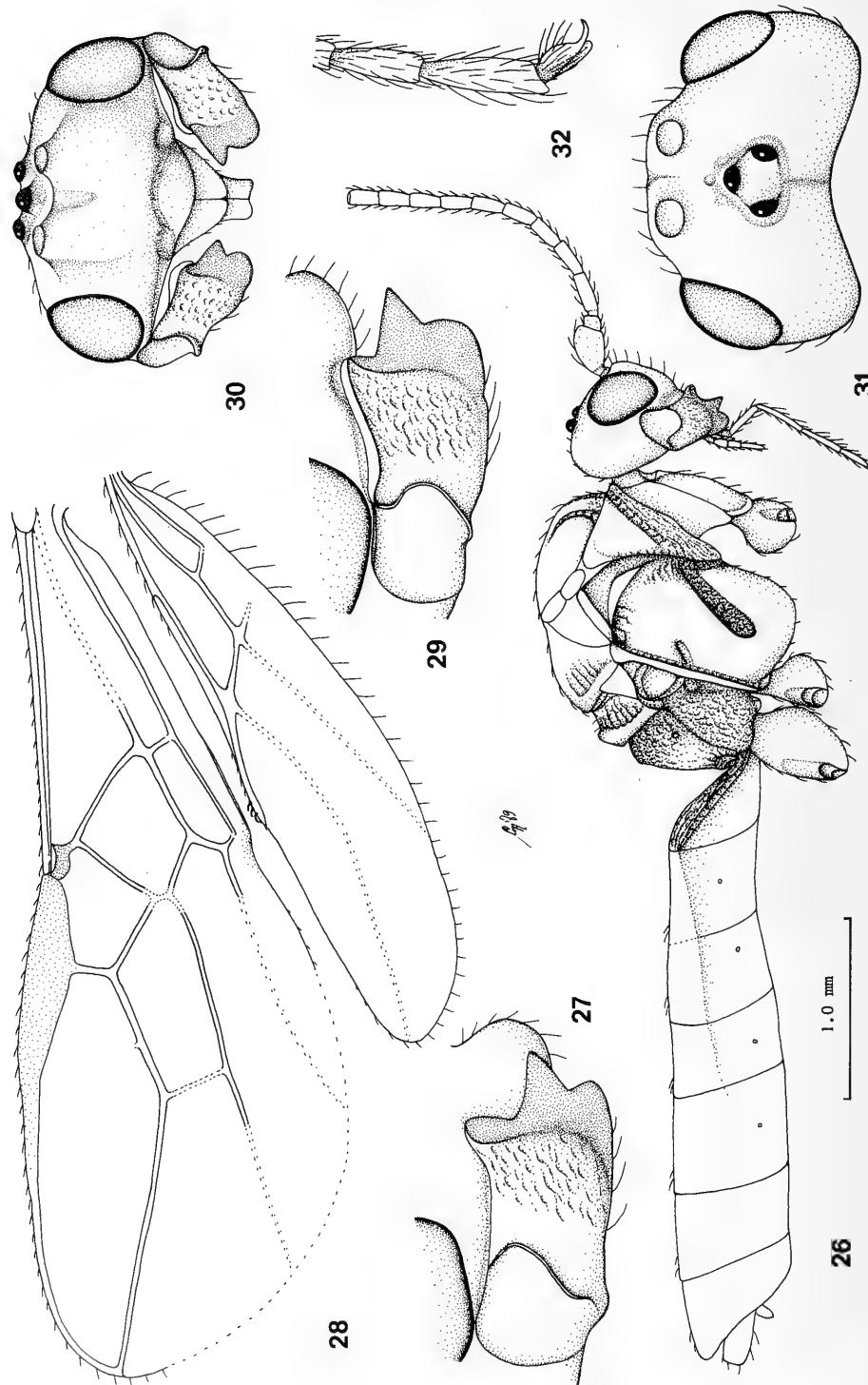
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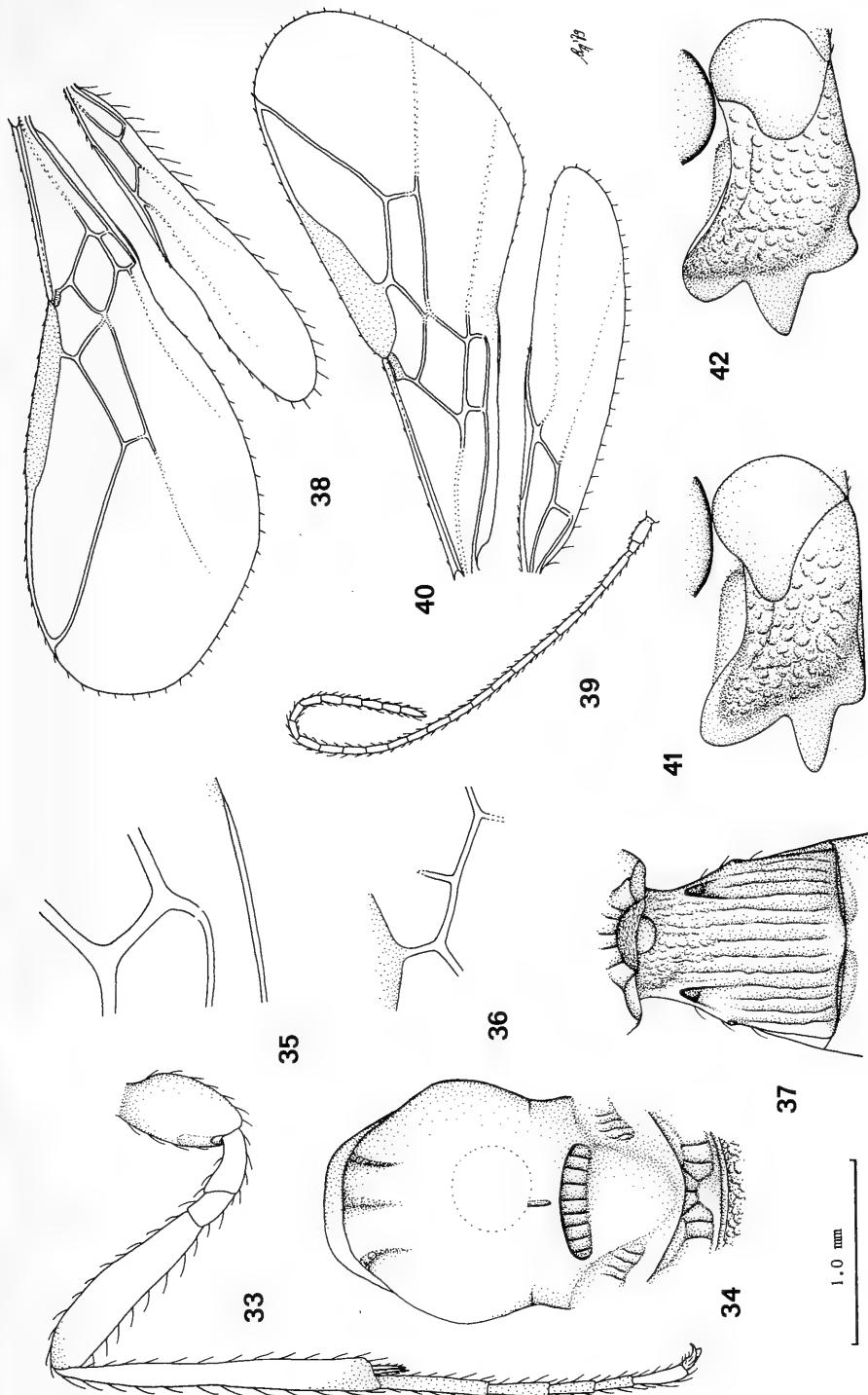
Figs. 1-14. *Adelurola florimela* (Haliday), ♀, Netherlands, Linschotterbos (but 15 from ♂, Netherlands, Waarder). 1, Habitus, lateral aspect; 2, detail of 3rd and 4th antennal segments; 3, head, frontal aspect; 4, mesonotum, dorsal aspect; 5, apex of antenna; 6, wing; 7, 1st tergite, dorsal aspect; 8, detail of veins CU1b and 3-CU1 of fore wing; 9, head, dorsal aspect; 10, inner hind claw; 11, hind leg; 12, mandible, full sight on 3rd tooth; 13, mandible, full sight on 1st teeth; 14, apical half of wing. 1, 6, 11, 14: scale-line, 1 ×; 2-4, 7-9: 1.6 ×; 5, 10, 12, 13: 4 ×.



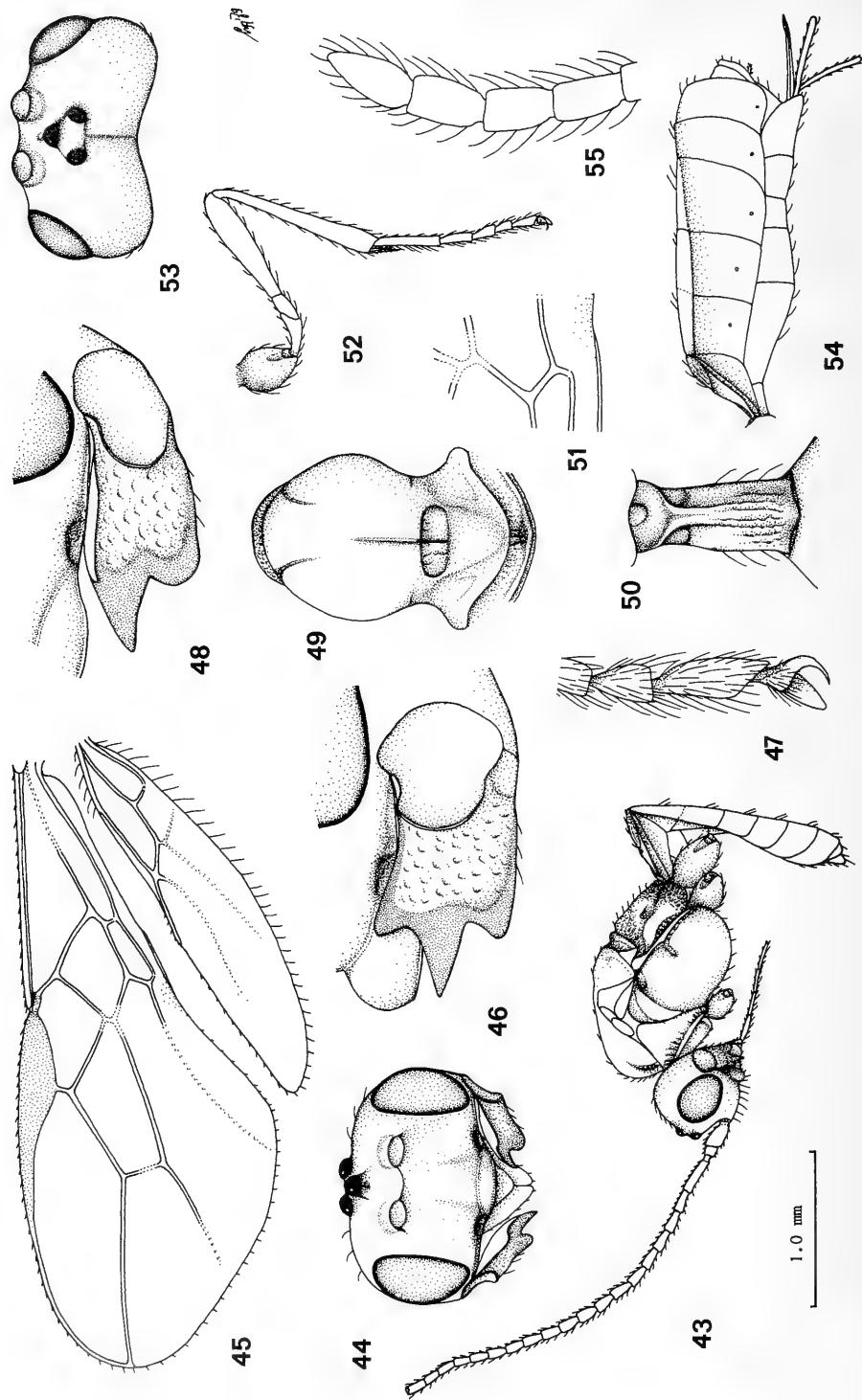
Figs. 15—25. *Dapsilarthra (Heterolexis) gahani* (Baume-Pluvine), lectotype. 15, habitus, lateral aspect; 16, head, frontal aspect; 17, wings; 18, 1st tergite, dorsal aspect; 19, mandible, full sight on 3rd tooth; 20, apex of antenna; 21, head, dorsal aspect; 22, inner middle claw; 23, hind leg; 24, thorax, dorsal aspect; 25, mandible, full sight on 1st tooth. 15, 17, 23; scale-line, 1 x; 16, 18, 21, 24: 16 x; 19, 20, 22, 25: 1.1 x.



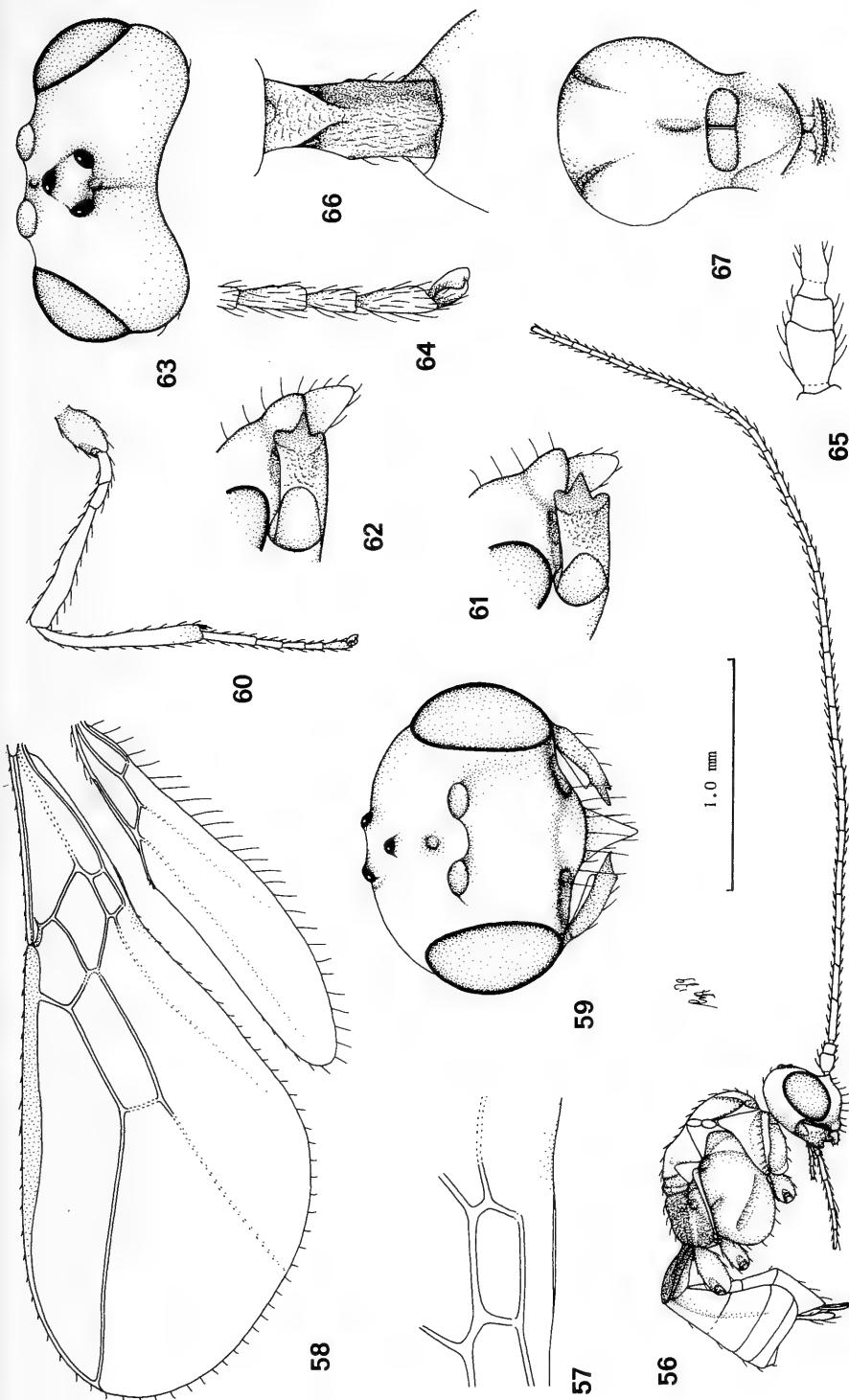
Figs. 26—32. *Dapsilarthra (Mesocirne) dalhousiensis* (Sharma), holotype. 26, habitus, lateral aspect; 27, mandible, full sight on 1st tooth; 28, right wings; 29, mandible, full sight on 3rd tooth; 30, head, frontal aspect; 31, head, dorsal aspect; 32, outer hind claw. 26, 28: scale-line, 1 X; 27, 29, 32: 2.5 X; 30, 31: 1.5 X.



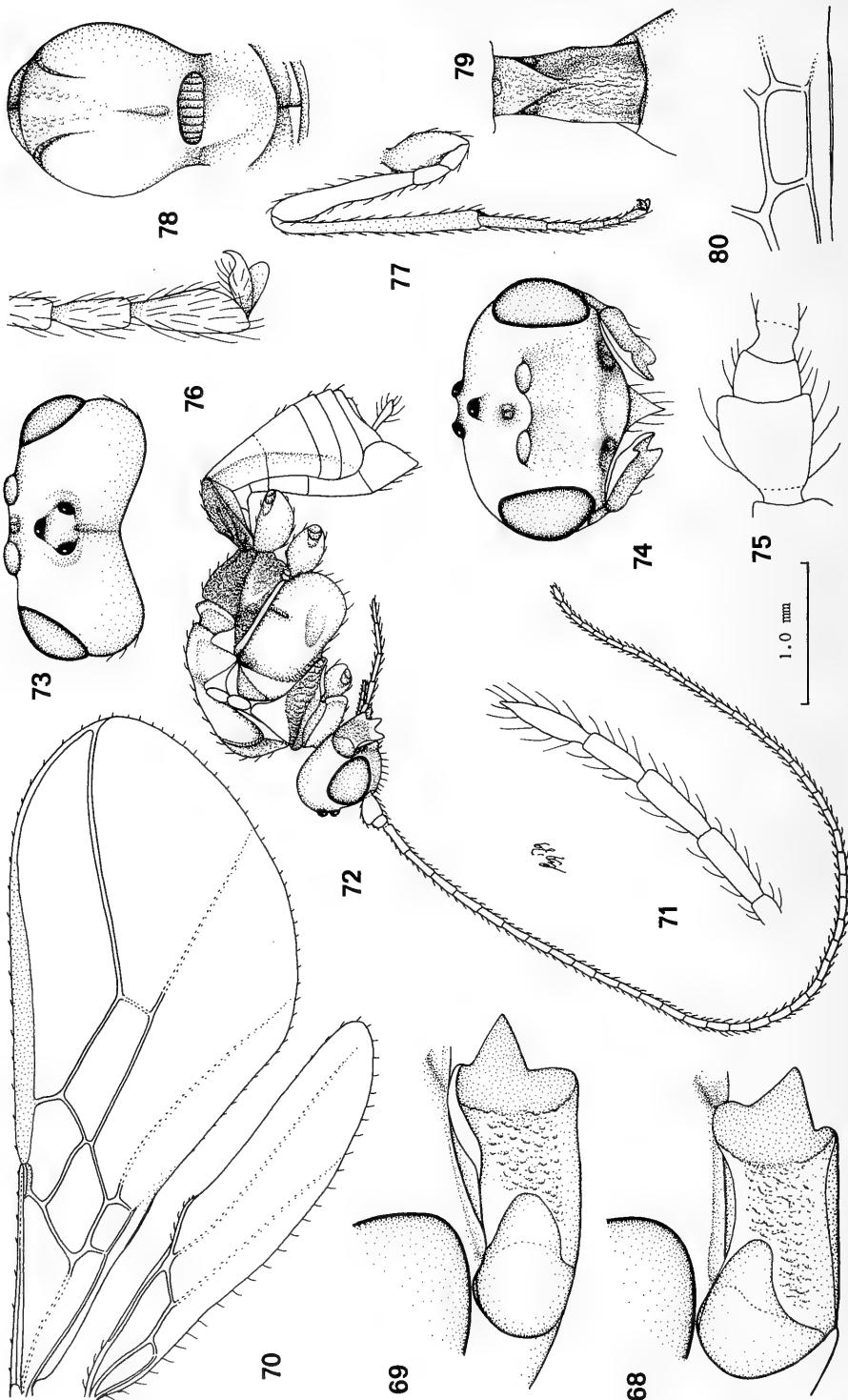
Figs. 33—37. *Dapsilarthra (Mesocrina) dalbousiensis* (Sharma), holotype 33, detail of veins 3-CU1 and CU1b of fore wing; 35, detail of vein 3-SR of left fore wing; 37, 1st tergite, dorsal aspect. Figs. 38—39. *Dapsilarthra (Dapsilarthra) tirolensis* (Königsmann), holotype. 38, wings; 39, antenna. Figs. 40—42. *Adelurola amplidens* (Fischer), paratype. 40, wings; 41, mandible, full sight on 1st tooth; 42, mandible, full sight on 3rd tooth. 33, 36: scale-line, 1 X; 34, 35, 37: 1.5 X; 38, 39: 1.6 X; 40, 42: 3.1 X.



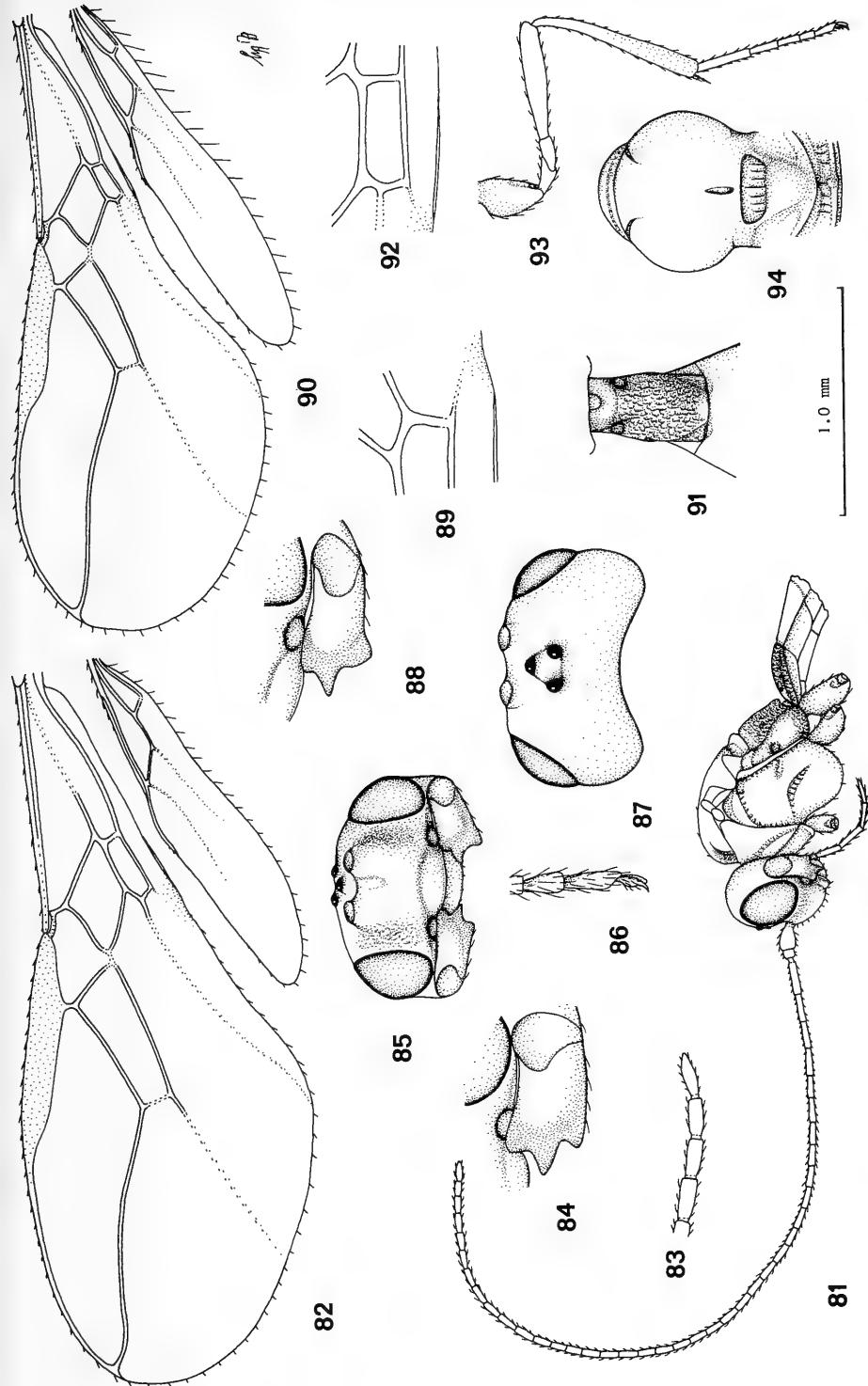
Figs. 43—55. *Dapsilarthra (Mesocrina) indagatrix* (Foerster), neotype (but 54—55 from ♀, Netherlands, Ede). 43, habitus, Ede. 44, head, frontal aspect; 45, wings; 46, mandible, full right on 1st tooth; 47, inner hind claw; 48, mandible, full sight on 3rd tooth; 49, thorax, dorsal aspect; 50, 1st tergite, dorsal aspect; 51, detail of veins 3-CU1 and CU1b of fore wing; 52, head leg; 53, hind leg; 54, mesosoma, lateral aspect; 55, apex of antenna. 43, 45, 52, 54: scale-line; X; 44, 49—51, 53—55: 2 X; 46—48, 55: 5 X.



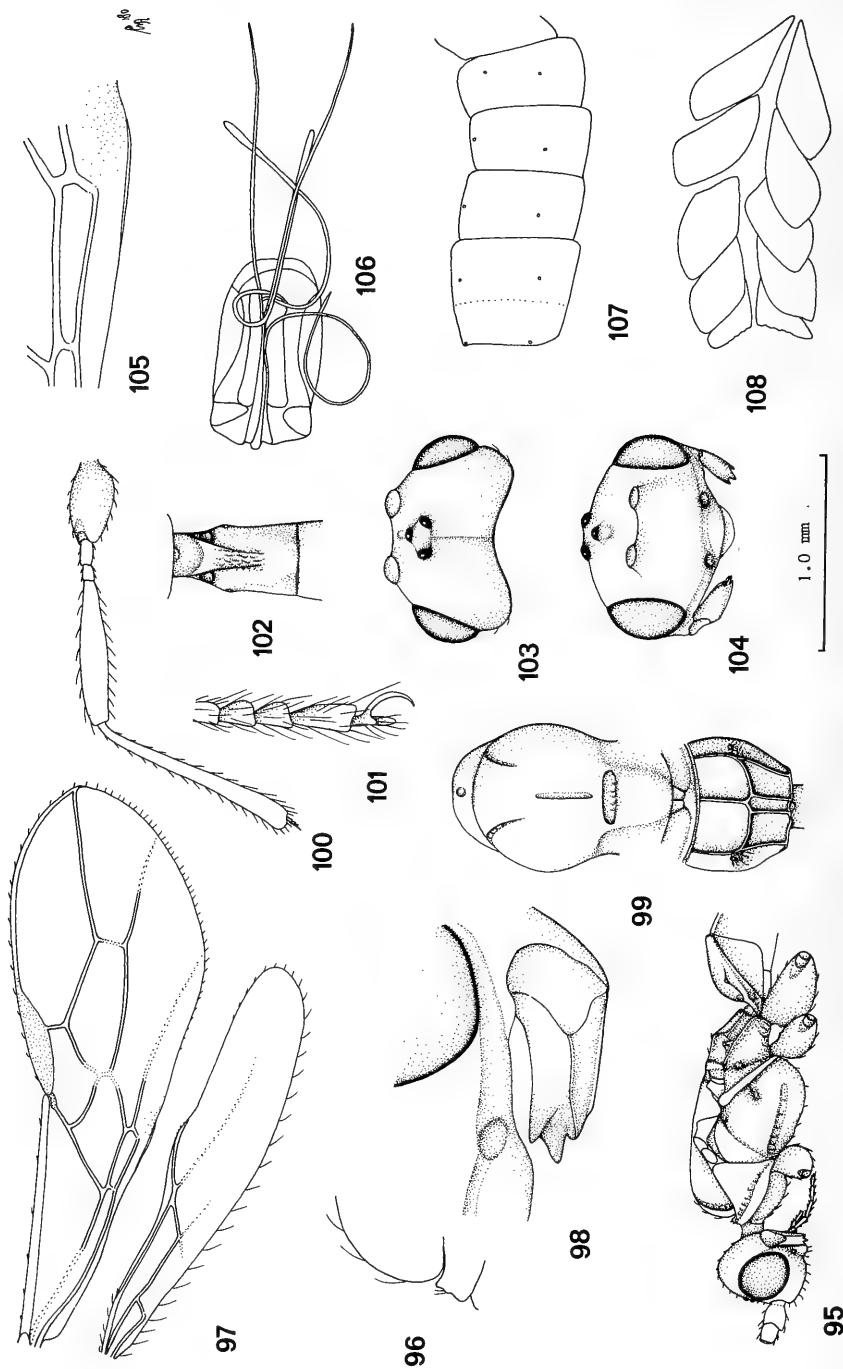
Figs. 56—67. *Dapsilarthra (Dapsilarthra) carpathica* spec. nov., holotype. 56, habitus, lateral aspect; 57, detail of veins 3-CU1 and CU1b of fore wing; 58, wings; 59, head, frontal aspect; 60, hind leg; 61, mandible, full sight on 3rd tooth; 62, mandible, full sight on 1st tooth; 63, head, dorsal aspect; 64, outer hind claw; 65, detail of scapus and pedicellus, lateral aspect; 66, 1st tergite, dorsal aspect; 67, mesonotum, dorsal aspect. 56, 58, 60: scale-line, 1  $\times$ ; 57, 59, 61—63, 66, 67: 2.5  $\times$ ; 64: 2.8  $\times$ ; 65: 3  $\times$ .



Figs. 68—80. *Dapsilatbra (Dapsilatbra) apii* (Curtis), ♀, Austria, Aschbach. 68, mandible, full sight on 1st tooth; 69, id., full sight on 3rd tooth; 70, wings; 71, apex of antenna; 72, habitus, lateral aspect; 73, head, dorsal aspect; 74, head, fronto-lateral aspect; 75, head, dorsal aspect; 76, detail of scutum and pedicellus; 77, hind leg; 78, thorax, dorsal aspect; 79, 1st tergite, dorsal aspect; 80, detail of vein 3-CU1 and CU1b of fore wing. 68, 69, 71, 75, 76: 5 ×; 70, 72, 77: scale line, 1 ×; 73, 74, 78—80: 2 ×.



Figs. 81—89, 91, 93—94. *Dapsilarthra (Dapsilarthra) isabella* (Haliday), ♀, England, Barnstaple. 81, habitus, lateral aspect (apex of metasoma removed); 82, wings; 83, apex of antenna; 84, mandible, full sight on 1st tooth; 85, head, frontal aspect; 86, outer hind claw; 87, head, dorsal aspect; 88, mandible, full sight on 3rd tooth; 89, detail of veins 3-CU1 and CU1b of fore wing; 91, 1st tergite, dorsal aspect; 93, hind leg; 94, thorax, dorsal aspect. Figs. 90, 92, *Dapsilarthra (Dapsilarthra) rufiventris* (Nees), ♀, Netherlands, Waarder. 90, wings; 92, detail of veins 3-CU1 and CU1b of fore wing. 81, 82, 93: scale-line, 1 ×; 83, 84, 86, 88, 89: 2.5 ×; 85: 1.6 ×; 87, 91, 94: 1.7 ×; 90: 1.5 ×; 92: 3.8 ×.



Figs. 95—108. *Prorima thienemanni* (Bischoff), holotype. 95, habitus, lateral aspect (metasoma largely removed); 96, detail of antescutal depression, lateral aspect; 97, wings; 98, mandible, full sight on 3rd tooth; 99, mesosoma, dorsal aspect; 100, hind leg; 101, inner middle claw; 102, 1st tergite, dorsal aspect; 103, head, dorsal aspect; 104, head, frontal aspect; 105, detail of 1st subdiscal cell of fore wing; 106, genitalia; 107, dissected tergites; 108, dissected sternites. 95, 97, 100, 106—108: scale-line, 1 ×; 96, 101, 105: 2.5 ×; 98: 3.7 ×; 99, 102—104: 1.5 ×.

# REVISIONARY NOTES ON THE SUBFAMILY GNAPTODONTINAE, WITH DESCRIPTION OF ELEVEN NEW SPECIES (HYMENOPTERA, BRACONIDAE)

by

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## ABSTRACT

The tribe *Gnaptogastrini* Tobias, 1976, is synonymized with the tribe *Gnaptodontini* Fischer, 1970, and the group is given subfamily rank. The genera *Gnaptogaster* Tobias, 1976, and *Gnaptodon* Haliday, 1837, are redescribed and illustrated. A neotype for *Bracon pumilio* Nees, 1834, (type-species of *Gnaptodon*) is selected, described and illustrated. A lectotype is designated for *Diraphus pygmaeus* Wesmael, 1838. Keys are given to the Palaearctic and Afrotropical species of *Gnaptodon*, of which eight new Palaearctic and two new Afrotropical species are described; additionally the first Oriental *Gnaptodon* species is described. *Mesotages* Foerster, 1862, is synonymized with *Gnaptodon* Haliday, 1837, and *Mesotages decoris* Foerster, 1862, is a new senior synonym of *G. bachmaieri* Fischer, 1957, and of *G. klemensiewiczi* (Niezabitowski, 1910). The ecology of the reared Palaearctic *Gnaptodon* species and the phylogenetic relationships of the Gnaptodontinae are discussed.

## INTRODUCTION

The genus *Gnaptodon* contains some of the smallest Braconidae, usually scarcely longer than 1 mm and exclusively parasites of the mining caterpillars of Nepticulidae (Lepidoptera). *Gnaptodon* and its relatives are recognizable by the peculiar basal elevation of the 2nd tergite (figs. 8, 31). However, in a new species described in this paper both the elevation and the 2nd suture of the metasoma are absent (fig. 19). Owing to a fine collection of parasites of Nepticulidae assembled by Dr. G. Bryan and Mr. E. J. van Nieuwerken (Vrije Universiteit, Amsterdam) and the *Gnaptodon* species reared by Dr. J. Szöcs (Budapest) it has been possible to revise the Palaearctic species of *Gnaptodon*. The *breviradialis* group (only described species: *breviradialis*) could be sorted out, resulting in six new species.

Tobias (1979: 240) on the basis of his material (which was not available for this study) concluded that all described Palaearctic forms actually belong to one large polymorphic species with enormous variation: *G. pumilio* (Nees). I agree with Tobias that the degree of sculpture and the colour alone are inadequate and often very variable character-states. However, the wing venation, the setosity, the shape of the grooves of the metasoma and (to some extent) coloration appear to allow of the recognition of

several species, and a study of the available reared series has confirmed the usefulness of these characters.

Additionally the opportunity is taken to synonymize the tribe *Gnaptogastrini* Tobias, 1976, with the Gnaptodontinae, to redescribe the genus *Gnaptogaster* Tobias, 1976, and to describe two new species of *Gnaptodon* from Africa (S. Africa and Somalia) and one new species from Thailand. In the cosmopolitan genus *Gnaptodon* 21 valid species have been described and in this paper 11 species are added. The generic combinations of the host species mentioned in this paper are on behalf of Mr. E. J. van Nieuwerken (Amsterdam), who is currently studying the biosystematics of the Nepticulidae. If the genus is given in inverted commas then the generic placement is uncertain. For the terminology used in this paper, see Van Achterberg (1979: 242—246, figs. 1—8).

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#### Subfamily GNAPTDONTINAE Fischer stat. nov.

*Gnaptodonina* Fischer, 1970: 85, 87.

*Gnaptodontini* Fischer, 1972: 55—57.

*Gnaptogastrini* Tobias, 1976a: 319. **Syn. nov.**

**Diagnosis.** — Length of fore wing 1.2—1.9 mm.; antennal segments 14—26; maxillary palp with 5 or 6 segments; labial palp with 3 segments; scapus truncate apically, stout (figs. 10, 22); hypostomal, occipital, and prepectal carinae usually absent, but occipital carina present in *Liparophleps* Enderlein and *Gnaptodon novobritanicus* Fischer, and prepectal carina present in *Liparophleps*; eyes glabrous, slightly or not emarginate; antennal sockets closer to eyes than to each other (fig. 32); anterior tentorial pits rather small and deep; clypeus (largely) smooth, rather convex; apical margin of clypeus slightly concave (fig. 14); hypoclypeal depression present, transverse, but labrum (nearly) flat and glabrous; malar suture absent; length of malar space 1.0—1.5 times basal width of mandible; mandible slender, twisted apically and 1st tooth much longer than 2nd; pronope, antescutal depression, lateral carina of mesoscutum, precoxal sulcus (except for a medial pit as in *Gnaptogaster*, fig. 1) absent; posterior flange of propleuron virtually absent; notauli reduced posteriorly (figs. 9, 18); episternal scrobe narrow (fig. 10); metapleural flange small or absent; scutellum completely smooth; metanotum at most with a short antero-medial carina, posteriorly smooth and rather convex, not distinctly protruding (fig. 22); propodeum smooth, without any areolation or carinae; propodeal spiracle round, rather small and in front of middle of propodeum; propodeal tubercle absent; 1st discal cell of fore wing petiolate; vein  $M + CU_1$  of fore wing completely sclerotized; vein  $cu-a$  of both wings present, short (figs. 3, 24); veins  $CU_1b$  and  $2-1A$  of fore wing more or less reduced, resulting in a partly open 1st subdiscal cell (figs. 3, 24); parastigma small (fig. 13) or medium-sized (fig. 3); vein  $m-cu$  of fore wing antefurcal and parallel to vein  $1-M$ ; veins  $2A$  and  $2-R_1$  of fore wing absent; vein  $SR$  of hind wing largely absent apically (figs. 3, 24); vein  $M + CU$  of hind wing shorter than vein  $1-M$ ; length of vein  $3-SR$  of fore wing 0.2—0.7 times vein  $2-SR$ ; tarsal claws slender apically,

simple, without lobe or pectination (fig. 2); spurs of hind tibia subequal, their length 0.2—0.3 times the basitarsus; fore tibia without spines or pegs; 1st metasomal tergite sessile, rather flat medio-basally (at least in the Oriental and Palaearctic species); spiracles of 1st tergite submedial or behind middle (figs. 1, 8, 19, 31); laterope absent (fig. 1) or small and pit-shaped (fig. 22); 2nd tergite with a curved basal elevation (figs. 8, 31), except in *Gnaptodon apehes* spec. nov. (fig. 19) which has only weak lateral traces; 2nd intersegmental suture of metasoma distinctly impressed, except in *G. apehes* spec. nov. (fig. 19); spiracles situated in notum of 2nd and 3rd metasomal tergites; metasoma depressed; ovipositor almost straight (fig. 1, 22); length of ovipositor sheath in Palaearctic and Oriental species 0.03—0.12 times fore wing.

Contains 4 genera: *Gnaptodon* Haliday, 1837 (cosmopolitan), *Pseudognaptodon* Fischer, 1965 (New World, possibly only a subgenus of *Gnaptodon*), *Gnaptogaster* Tobias, 1976 (Palaearctic), and (provisionally included) *Liparophleps* Enderlein, 1920 (Neotropical).

#### KEY TO GENERA OF THE SUBFAMILY

#### GNAPTDONTINAE

1. Occipital and prepectal carinae present . . . . . *Liparophleps* Enderlein (Synonym of *Plesademon* Fischer, 1961; may belong to the Doryctinae, but lacks the characteristic pegs of the fore tibia).
- Occipital and prepectal carinae absent, at most with a faint trace of the occipital carina present . . . . . 2
2. Vein  $r-m$  of fore wing absent . . . . . *Pseudognaptodon* Fischer
- Vein  $r-m$  of fore wing present (as an un sclerotized, slightly pigmented vein, figs. 3, 13) . . . . . 3
3. Dorsal carinae of 1st tergite absent (fig. 8); mesoscutal pit present (fig. 9); apex of antenna without short spine (fig. 4); pleural sulcus crenulate (fig. 1); maxillary palp with 5 segments . . . . . *Gnaptogaster* Tobias
- Dorsal carinae of 1st tergite present (figs. 19, 31); mesoscutal pit absent (fig. 18); apex of antenna with short spine (fig. 11); pleural sulcus smooth (fig. 10); maxillary palp with 6 segments (fig. 16) . . . . . *Gnaptodon* Haliday

#### Genus *Gnaptogaster* Tobias, 1976

*Gnaptogaster* Tobias, 1976a: 319.

Type-species: *Gnaptogaster mongolica* Tobias, 1976. Gender: feminine.

**Diagnosis.** — Length of fore wing ca. 1.8 mm, length of body ca. 2.1 mm; antennal segments 18—20; apex of antenna without spine apically (fig. 4); maxillary palp with 5 segments; occipital carina completely absent; marginal cell of fore wing very narrow (fig. 3); apical margin of clypeus not differentiated from clypeus (fig. 6); mesopleuron smooth, except for the medial pit (fig. 1); mesoscutal pit present (fig. 9); notaui shallow, finely crenulate, but posteriorly absent (fig. 9); pleural sulcus crenulate (fig. 1); dorsal carinae of 1st metasomal tergite absent (fig. 8); basal elevation of 2nd tergite distinctly differentiated by the curved groove (fig. 8); length of ovipositor sheath ca. 0.06 times fore wing.

Contains only the East Palaearctic type-species.

### ***Gnaptogaster mongolica* Tobias, 1976**

(figs. 1—9)

*Gnaptogaster mongolica* Tobias, 1976a: 319—321, figs. 2—5.

Paratype, ♀, length of body 2.1 mm, of fore wing 1.8 mm.

**Head.** — Antennal segments 19, 3rd segment 1.2 times 4th segment, length of 3rd and 4th segment 2.3 and 2.0 times their width, respectively, penultimate segment 2.1 times its width; length of maxillary palp 0.5 times height of head; length of eye 2.6 times temple in dorsal view; POL: Ø ocellus: OOL = 10 : 5 : 8; frons concave behind antennal sockets, smooth; vertex rather flat and finely granulate near stemmaticum; face convex and smooth; epistomal suture present, but medially shallow (fig. 6); length of malar space equal to basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.3 times its height; side of pronotum smooth, except for a narrow crenulate area posteriorly (fig. 1); metapleuron smooth; middle lobe of mesoscutum with weak medial suture (fig. 8); mesoscutum smooth; scutellar sulcus medium-sized, rather shallow, with 4 weak longitudinal carinae; scutellum rather convex, smooth; surface of propodeum smooth; medial carina absent.

**Wings.** — Fore wing: r : 3-SR : SR1 = 4 : 5 : 34; 1-CU1 : 2-CU1 = 5 : 23; 2-SR : 3-SR : r-m = 17 : 5 : 14; m-cu far antefurcal (fig. 3). Hind wing: m-cu present as a weak, unpigmented trace (fig. 3).

**Legs.** — Length of femur, tibia, and basitar-

sus of hind leg 3.3, 6.1 and 6.0 times their width, respectively (fig. 5).

**Metasoma.** — Length of 1st tergite 0.6 times its apical width, its surface smooth, basally rather flat, medially convex, and laterally rather flattened (fig. 8); spiracles of 1st tergite after middle of tergite and not protruding (fig. 8); glymma completely absent; 2nd tergite smooth and 2nd intersegmental suture deep and smooth; all metasomal setae widely spaced, scattered; 2nd and 3rd segments with a sharp lateral crease; length of ovipositor sheath 0.06 times fore wing.

**Colour.** — Black; legs (but hind coxa blackish basally and hind tarsus somewhat infuscated), tegulae, palpi, mandibles, scapus and antennellus mainly, and metasoma (but apically infuscated), yellowish-brown; pterostigma dark brown, wing membrane hyaline.

**Holotype and paratypes** in the Zoological Institute, Leningrad. The figured and redescribed paratype is topotypic with the holotype: "Mongolia, South Gobijskij ajmak, 20 km. West of well of Barin-Bugatyn-Khuduk, Kerzhner, 25—27.vii.1969" (translated), "Paratype *Gnaptogaster* (sic!) *mongolica* Tobias".

**Note.** — Tobias erected a separate tribe for his *Gnaptogaster*, but this is evidently unnecessary. It fits well into the *Gnaptodontinae* because it shares several synapomorphous character-states with *Gnaptodon*. For example, the curved basal elevation of the 2nd tergite, the short 2nd submarginal cell of the fore wing, the 3-segmented labial palp, the narrow and shallow hypoclypeal depression, and the (nearly) flat and glabrous labrum.

### **Genus *Gnaptodon* Haliday, 1837**

*Gnaptodon* Haliday, 1837: 220. Fischer, 1972: 569.

Shenefelt, 1975: 1123. Tobias, 1976a: 315—318;

1976b: 22, 47. Marsh, 1979: 173.

*Diraphus* Wesmael, 1838: 89. Fischer, 1972: 569.

Shenefelt, 1975: 1123. Marsh, 1979: 173.

*Mesotages* Foerster, 1862: 258. *Syn. nov.*

**Type-species:** *Bracon pumilio* Nees, 1834.  
Gender: masculine.

**Diagnosis.** — Length of fore wing and of body, both 1.0—1.9 mm; antennal segments 14—26; apex of antenna with short spine (fig. 11); maxillary palp with 6 segments (fig. 28); apical margin of clypeus narrowly differentiated from clypeus (fig. 14); mesopleuron completely

smooth, exceptionally precoxal sulcus superficially impressed; mesoscutal pit absent (fig. 18), exceptionally with a shallow impression; pleural sulcus smooth (fig. 10); notauli of Palaearctic and Oriental species smooth, and posteriorly (nearly) absent (figs. 18, 26); dorsal carinae of 1st tergite basally present (figs. 19, 31); length of ovipositor sheath of Palaearctic and Oriental species 0.03—0.12 times length of fore wing.

**Biology.** — The larvae are obligatory parasites of (mining) larvae of Nepticulidae (Lepidoptera). Pupation takes place in the host cocoon, but endoparasitism remains to be proven (see chapter on phylogenetic relationships).

**Distribution:** Palaearctic: 12 species; Nearctic: 7 species; Neotropical: 1 species; Afrotropical: 3 species; Oriental: 1 species; Australian: 8 species.

#### A. PALAEARCTIC REGION

##### KEY TO THE PALAEARCTIC SPECIES OF THE GENUS *GNAPTODON* HALIDAY

1. Second intersegmental suture of metasoma deep medially (figs. 31, 43, 51); transverse elevation of 2nd tergite distinct medially (figs. 31, 63), exceptionally obsolete (fig. 102); colour of 3rd antennal segment variable, if dark brown, then hind femur yellowish ..... 2
- Second suture (almost) absent (fig. 19); transverse elevation of 2nd tergite absent medially (fig. 19); 3rd antennal segment dark brown; hind femur largely dark brown ..... *apheles* spec. nov.
2. Distance between wing apex and apex of marginal cell 1.5—3.6 times vein 1-R1 (figs. 57, 65, 74, 91); length of pterostigma 1.5—3.0 times vein 1-R1; intermediate specimens have posterior margin of elevation of 2nd tergite weakly curved or straight medially (figs. 63, 80) and metasoma of ♀ comparatively robust (fig. 110) ..... 3
- Distance between wing apex and apex of marginal cell 0.2—1.4 times vein 1-R1 (figs. 20, 24), exceptionally up to 1.8 times (fig. 46); length of pterostigma 0.7—1.9 times vein 1-R1; intermediate specimens have posterior margin of elevation of 2nd tergite distinctly curved (figs. 51, 53) and metasoma of ♀ comparatively slender (fig. 53) .. 9
3. Vein r of fore wing about as long as vein 3-SR or longer (fig. 91); antero-lateral grooves of 3rd tergite rather deep (exceptionally obsolete) and (very) finely crenulate (fig. 92); vertex (largely) smooth; antennal segments 17—19 ..... *breviradialis* Fischer
- Vein r of fore wing shorter than vein 3-SR (fig. 74, 84); antero-lateral grooves of 3rd tergite absent or shallow and smooth (figs. 72, 80); vertex often coriaceous; antennal segments 18—23 ..... 4
4. Marginal cell of fore wing narrow (fig. 57); distance between wing apex and apex of marginal cell about 3 times vein 1-R1 (fig. 57); metasoma completely yellowish; length of vein SR1 of fore wing about 3 times vein 3-SR (fig. 57); episternal scrobe deep (fig. 55); ocelli small, POL 2.5—3 times diameter of posterior ocellus (fig. 56); medial length of 2nd tergite about 1.5 times medial length of 3rd tergite (fig. 63) ..... *brevis* spec. nov.
- Marginal cell of fore wing wider (figs. 65, 96); distance between wing apex and apex of marginal cell 1.5—2.2 times vein 1-R1; colour of metasoma variable; length of vein SR1 of fore wing 4.0—6.7 times vein 3-SR (figs. 74, 96); episternal scrobe rather shallow or obsolete (fig. 94); ocelli larger, POL about twice diameter of posterior ocellus or shorter (figs. 93, 98); medial length of 2nd tergite less than 1.5 times medial length of 3rd tergite (figs. 80, 85) ..... 5
5. Vertex almost completely smooth and strongly shiny (fig. 71); 3rd tergite with shallow and smooth antero-lateral grooves (fig. 72); 1st and 2nd tergites, antero-lateral corners and hind tarsi (except telotarsus), ivory-whitish; 2nd suture of metasoma distinctly crenulate medially (fig. 72); vein SR1 of fore wing straight (fig. 65) ..... *vlugi* spec. nov.
- Vertex coriaceous, moderately shiny (fig. 83); 3rd tergite with no antero-lateral grooves (figs. 80, 102), colour and vein SR1 variable; 2nd suture smooth or indistinctly crenulate (figs. 80, 102) ..... 6
6. Long dense setose between antennal sockets (figs. 76, 77); medio-longitudinal groove of mesoscutum anteriorly as deep as notauli (fig. 81); medial length of 3rd tergite equal to medial length of 2nd tergite (fig. 80) or slightly less; 2nd tergite dark brown posteriorly ..... *pilosus* spec. nov.
- Sparsely setose between antennal sockets (fig. 83); medio-longitudinal groove of mesoscutum anteriorly shallower than no-

- tauli (figs. 82), 100); medial length of 3rd tergite variable (figs. 85, 110); 2nd tergite frequently completely yellowish ..... 7
7. Hind coxa at least basally and hind femur dorso-apically infuscated; 2nd tergite posteriorly and hind tarsus dark brown; medial length of 3rd tergite of ♀ 1.1—1.3 times medial length of 2nd tergite (fig. 85); marginal cell of fore wing comparatively narrow (fig. 84), distance between wing apex and apex of marginal cell 1.9—2.4 times vein 1-R1; face (except medially) densely and transversely rugulose-coriaceous .....  
..... *nieuwkerkeni* spec. nov.
- Hind coxa, hind femur apically, 2nd tergite posteriorly and hind tarsus (except telotarsus), yellowish; medial length of 3rd tergite of ♀ 0.7—0.8 times medial length of 2nd tergite (figs. 102, 110); marginal cell of fore wing somewhat wider (figs. 96, 104), distance between wing apex and apex of marginal cell 1.6—1.9 times vein 1-R1; face coriaceous or smooth ..... 8
8. Head and apical half of metasoma yellowish; 2nd suture of metasoma rather angularly bent (fig. 102); pterostigma and 3rd and 4th antennal segments dark brown; antennal segments of ♀ about 21; scutellar sulcus distinct (fig. 100) ..... *ruficeps* spec. nov.
- Head and apical half of metasoma black; 2nd suture of metasoma rather evenly curved (fig. 110); pterostigma light brown; 3rd and 4th antennal segments of ♀ about 18; scutellar sulcus very shallow (fig. 107) ..  
..... *erasmi* spec. nov.
9. Distance between wing apex and apex of marginal cell of fore wing 0.2—0.5 times vein 1-R1 (fig. 24); vein SR1 of fore wing largely straight (fig. 24); area behind transverse elevation of 2nd tergite often more or less sculptured (fig. 31) ..... 10
- Distance between wing apex and apex of marginal cell of fore wing 0.7—1.8 times vein 1-R1 (figs. 20, 46); vein SR1 rather sinuate (fig. 46); area behind elevation of 2nd tergite often largely smooth (figs. 51, 53)  
..... 11
10. Length of vein 1-R1 of fore wing 2—4 times distance between wing apex and apex of marginal cell of fore wing (fig. 24); 3rd antennal segment yellowish, exceptionally dark brown; mainly parasite of Nepticulidae in trees ..... *pumilio* (Nees)
- Length of vein 1-R1 of fore wing about 5 times distance between wing apex and apex of marginal cell of fore wing (fig. 96 in Fischer, 1966); 3rd antennal segment dark brown .....  
..... *nepalicus* Fisher
11. Four basal segments of antenna of ♀ infuscated or dark brown dorsally, exceptionally (largely) yellowish; medial length of basal elevation of 2nd tergite less than 0.6 times medial length of rest of tergite or, if longer, less narrowed laterally (cf. fig. 31); medio-longitudinal groove of mesoscutum often distinct; metasoma usually dark brown or black, if partly yellowish then elevation of 2nd tergite indistinct medially; antennal segments of ♀ mostly 21; parasites of Nepticulidae in herbs and (low) shrubs .....  
..... *decoris* (Foerster)
- Four basal antennal segments of ♀ yellowish; medial length of basal elevation of 2nd tergite 0.6—1.0 times medial length of rest of tergite and elevation distinctly narrowed laterally (figs. 51, 53); medio-longitudinal groove of mesoscutum usually obsolete (fig. 49); several tergites of metasoma yellowish; basal elevation of 2nd tergite distinct medially; antennal segments of ♀ usually 19 or 20; parasites of Nepticulidae in trees and (tall) shrubs ..... *georginae* spec. nov.

Note. — Of the 7 Nearctic species, 3 are close to Palaearctic spp.: *Gnaptodon bicolor* Fischer, 1965, is near *erasmi*, but *bicolor* has length of mesosoma about 1.5 times its height and distance between apex of fore wing to apex of marginal cell about 1.5 times vein 1-R1 (fig. 876 in Fischer, 1977). *G. glaber* Fischer, 1965, is close to *georginae* but the latter has infuscated hind tarsi, pterostigma dark brown, and face less sculptured. Finally *G. nepticulae* (Rohwer, 1915) (= *G. pulchrigaster* Fischer, 1965, according to Marsh, 1974) is close to *pumilio*, but *nepticulae* differs by the reddish base of the metasoma and the deep, crenulate, antero-lateral grooves of 3rd tergite. The only Neotropical species described, *G. novoteutonicus* Fischer, 1977, is exceptional because of its long ovipositor.

***Gnaptodon aphelis* spec. nov.**  
(figs. 10—19)

Holotype, ♀, length of body and of fore wing both 1.6 mm.

Head. — Antennal segments 20, length of 3rd segment 1.2 times 4th segment, length of 3rd and 4th segments 3.5 and 2.8 times their width

respectively, penultimate segment 1.7 times its width; length of maxillary palp 0.9 times height of head; length of eye 1.5 times temple in dorsal view; POL : Ø ocellus : OOL = 8 : 4 : 10; frons slightly convex, smooth; vertex convex, faintly coriaceous; face laterally coriaceous, shiny; length of malar space 1.5 times basal width of mandible.

Mesosoma. — Length of mesosoma 1.5 times its height; middle lobe of mesoscutum slightly impressed (fig. 18); scutellar sulcus rather narrow and shallow, and with one medial longitudinal carina besides the crenulae (fig. 18); episternal scrobe medium-sized (fig. 10).

Wings. — Fore wing: r : 3-SR : SR1 = 6 : 11 : 62; 1-CU1 : 2-CU1 = 1 : 9; 2-SR : 3-SR : r-m = 16 : 11 : 11; distance of wing apex to apex of marginal cell 0.5 times length of vein 1-R1; length of pterostigma 0.8 times length of vein 1-R1 (fig. 13); vein SR1 nearly straight (fig. 13).

Legs. — Length of femur, tibia and basitarsus of hind leg 4.4, 8.5, and 7.5 times their width, respectively.

Metasoma. — Length of 1st tergite equal to its apical width, its surface smooth, and dorsal carinae weakly developed in front of spiracles (fig. 19); 2nd tergite smooth, without distinct transverse elevation basally, except for some lateral traces (fig. 19); 2nd intersegmental suture absent; length of ovipositor sheath 0.06 times fore wing.

Colour. — Black; antenna, palpi, coxae, trochanters, middle and hind femora, tegulae, pterostigma, wing veins, and metasoma ventrally, dark brown; rest of legs yellowish brown; wing membrane hyaline.

Holotype in the Haeselbarth Collection, München: "St. Peter/Ahrntal, Südtirol, 1900 m, J/26.8.(19)67, Haeselbarth". Paratype: 1♀ (Rijksmuseum van Natuurlijke Historie, Leiden), topotypic, but from 2200 m. Antennal segments 20, length of fore wing 1.7 mm; length of ovipositor sheath 0.06 times fore wing; length of body 1.5 mm; other characters essentially as holotype.

Note. — The wing venation of *G. aphelis* is similar to the venation of *G. pumilio* (Nees), but *pumilio* differs (in addition to its sculptured 1st tergite, the distinct transverse groove of its 2nd tergite, and the deep 2nd suture of its metasoma) by its yellowish scapus, pedicellus, 3rd antennal segment, and its more extensive yellowish legs.

### **Gnaptodon breviradialis Fischer**

(figs. 91—93)

*Gnaptodon breviradialis* Fischer, 1959: 259; 1972: 571—572, fig. 435. Shenefelt, 1975: 1123. Tobias, 1976b: 48. Szócs, 1979: 200, 201.

Variation. — Antennal segments 17—19; length of fore wing and of body, both 1.4—1.8 mm; 4 or 5 basal antennal segments yellowish; vein r of fore wing about as long as vein 3-SR of longer (fig. 91); length of pterostigma 1.6—3 times vein 1-R1 of fore wing; distance between wing apex and apex of marginal cell of fore wing 2.1—3.6 times vein 1-R1; 3rd tergite with usually finely crenulate antero-lateral grooves, but these sometimes shallow and smooth; vertex smooth.

Specimens examined: Holotype, ♀, also 7 ♀ and 7 ♂. The examined specimens originate from France, Hungary and Greece.

Hosts. — Nepticulidae in the tree zone: in *Loranthus europaeus* Jacq. (in Greece collected from *Castanea* trees):

ex *Niepeltia loranthella* (Klimesch); Greece, Evvoia, Dhírfis Oros, 2 km NE Steni, 500 m, *Castanea-Abies* forest; id., S slopes of Dhírfis Oros, 700—900 m; Hungary, Normafa.

in *Ulmus* spec.:

ex *Stigmella ulmivora* (Folgone); France, Digne.

in *Prunus mahaleb* L.:

ex *Ectoedemia mahalebella* (Klimesch); Greece, Mt. Timfristos, Evritania, above Karpenission, *Spartium* shrub, 1200—1400 m.

in *P. cocomilia* Ten.:

ex *Stigmella amygdali* (Klimesch); Greece, 4 km NW Timfristós, (vill.), Fthiotis, 1400 m, clearings in *Abies* wood.

Tobias (1976b: 48) reported *breviradialis* from the European part of the U.S.S.R. and gives *Stigmella prunetorum* (Stainton) as host.

### **Gnaptodon brevis** spec. nov.

(figs. 55—63)

Holotype, ♀, length of body 1.4 mm, of fore wing 1.3 mm.

Head. — Antennal segments 20, length of 3rd segment 1.2 times 4th segment, length of 3rd and 4th segments 3.7 and 3.0 times their width, respectively, the penultimate segment 2 times its width (fig. 61); length of maxillary palp 0.8 times height of head; length of eye 1.6 times

temple in dorsal view (fig. 56); POL : Ø ocellus : OOL = 14 : 5 : 19; frons rather flat and coriaceous; vertex distinctly coriaceous, face medially smooth, otherwise coriaceous (fig. 62); length of malar space 1.5 times basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.2 times its height; medio-longitudinal depression of mesoscutum absent (fig. 60); scutellar sulcus rather shallow and medium-sized, crenulate (fig. 60); episternal scrobe deep (fig. 55).

**Wings.** — Fore wing : r : 3-SR : SR1 = 3 : 6 : 16; 1-CU1 : 2-CU1 = 1 : 8; 2-SR : 3-SR : r-m = 16 : 11 : 11; length of pterostigma 2.3 times vein 1-R1; distance between apex of fore wing and apex of marginal cell 3 times vein 1-R1 (fig. 57); vein SR1 straight.

**Legs.** — Length of femur, tibia and basitarsus of hind leg 3.1, 8.5, and 5.3 times their width, respectively.

**Metasoma.** — Length of 1st tergite 0.6 times its apical width, its surface superficially coriaceous (fig. 63), and dorsal carinae present in basal half of tergite; 2nd tergite behind basal elevation coriaceous, basal elevation smooth and distinctly transverse (fig. 63), its medial length 0.4 times medial length of rest of tergite; medial length of 2nd tergite 1.5 times 3rd tergite; 3rd and following tergites largely coriaceous, with no antero-lateral grooves; 2nd suture deep, curved and indistinctly crenulate; length of ovipositor sheath 0.12 times fore wing.

**Colour.** — Dark brown (including pterostigma and veins); antenna dark brown, but 3 basal segments ventrally yellowish; palpi, legs (but telotarsi infuscated), tegulae, and whole metasoma, yellowish; mesosoma laterally largely rather reddish; wing membrane slightly infuscated.

Holotype in Museum Budapest: "Budaörs, Törökugrato" (= Hungary), 1975.vii.16, Szöcs J., "Filipendula vulgaris", "ex *Nepticula hexapetalae* Szöcs".

Host: *Ectoedemia hexapetala* (Szöcs) in *Filipendula vulgaris* Moench.

### **Gnaptodon decoris** (Foerster) comb. nov. (fig. 20)

*Mesotages decoris* Foerster, 1862: 258.

*Gnaptodon bachmaieri* Fischer, 1957: 41. **Syn. nov.**  
*Gnaptodon bachmaieri*; Fischer, 1972: 570—571.  
Shenefelt, 1975: 1123. Tobias, 1976b: 48. Szöcs, 1979: 200—201.

*Gnaptodon bachmaieri* (sic!); Fischer, 1980: 202.

*Gnaptodon klemensiewiczii* Niezabitowski, 1910:  
44. Shenefelt, 1975: 1123—1124. **Syn. nov.**

**Variation.** — Antennal segments 20—23 (mostly 21); length of fore wing 1.2—1.7 mm, of body 1.1—1.7 mm; 5th—7th tergites of metasoma sometimes yellowish-brown, usually dark brown; length of pterostigma 1.0—1.6 (usually 1.1—1.2) times length of vein 1-R1; distance between apex of fore wing and apex of marginal cell 0.9—1.5 times vein 1-R1; 3rd antennal segment and base of metasoma dark brown, exceptionally yellowish; 2nd and 3rd tergites usually smooth, but sometimes superficially sculptured behind the transverse elevation and the 2nd metasomal suture; vertex coriaceous. Specimens examined: 22 ♀ and 29 ♂.

The examined specimens originate from Great Britain (Wales), Netherlands (Wijster, dunes of Meijendel (near the Hague) and of Oostvoorne, Kunrade (Kunderberg), and Hilversum (Spanderswoud)), West Germany, Italy, Austria, Hungary, Bulgaria and Greece.

**Hosts.** — Nepticulidae in herbs and (low) shrubs:

in *Lotus corniculatus* L.:

ex *Trifurcula cryptella* (Stainton); Netherlands, Kunrade, Kunderberg (2nd tergite dark brown and hind coxa infuscated).

in *Coronilla varia* L.:

from same host; Hungary, Svár.

in *Fragaria vesca* L.:

ex *Stigmella fragariella* (Heyd.) (on label, cf. *aurella* (F.)); Hungary, Budapest, Petneházi-rét (apex of metasoma reddish, rest of metasoma dark brown, hind coxa yellowish).

in *Sanguisorba officinalis* L.:

ex *S. geminella* (Frey) (on label, cf. *poterii* (Stainton)); Hungary, Fót, Mogyorodi p. (only 1st tergite and apex of metasoma dark brown, rest yellowish, hind coxa infuscated).

in *Rubus* spec.:

ex *S. splendidissimella* (H.-S.) or *aurella* (F.); Netherlands, Hilversum, Spanderswoud (2nd tergite yellowish).

in *Rosa pimpinellifolia* L.:

ex *S. spec.*; U.K., Wales, Pembrey, Carmarthen.

in *Agromonia agrimonoides* (L.):

ex *Ectoedemia agrimoniae* (Frey); Greece, Evvoia, Dhírfis Óros, S. slopes, *Castanea-Abies*-forest, 700—900 m (elevation of 2nd tergite largely absent, 2nd tergite and hind coxa yellowish).

in *Potentilla erecta* L.:

ex *Stigmella poterii* (Stainton); Hungary, Svár.

in *Potentilla* spec.:

ex *S. occultella* (Hein.) (on label, cf. *poterii* (Stainton)); Austria, Schörling, north of Attersee; id., Hinter-Stoder.

in *Prunus spinosa* L.:

ex *S. plagicolella* (Stainton); Hungary, Vérteskozma (aberrant because of yellowish 3rd and 4th antennal segments; 2nd tergite dark brown).

in *Betula nana* L.:

ex *S. betulicola nanivora* Petersen; West Germany (types of *G. bachmaieri* (Fischer), examined: 2nd tergite dark brown, hind coxa yellowish.

Notes. — The type of *Gnaptodon klemensiewiczii* Niezabitowski, 1910, was not available for study (it is part of a private collection; according to Tobias (1979: 237) the type is lost). Judging from the original description (1st and 2nd tergites smooth and 3rd antennal segment blackish) it is most likely to be a junior synonym of *G. decoris* (Foerster).

During my visits to the Berlin Museum I examined the holotype of *Mesotages decoris* Foerster, 1982. It is a completely yellowish specimen, probably owing to ageing (as many other small specimens in the Foerster collection are bleached). The length of the pterostigma is 1.5 times vein 1-R1 (metacarp) and the distance between the apex of the fore wing and the apex of the marginal cell is 1.4 times vein 1-R1. The vertex is distinctly coriaceous and the 2nd suture of the metasoma smooth. The basal elevation of the 2nd tergite is rather transverse. Foerster stated in the original description that the transverse elevation of the 2nd tergite is absent, but the surface of the 2nd tergite of the metasoma is obscured by some glue and by part of the hind wing. If looked for carefully the typical transverse elevation of the 2nd tergite can be seen. This explains how Foerster arrived at his incorrect statement in the original description and Fischer's description of this species as *bachmaieri*. The holotype of *decoris* in the Foerster Collection (Zoologisches Museum, Berlin) bears the following labels: "24/926", "Rheinprovinz", "Frst", "decoris Frst", "*Gnaptodon bachmaieri* Fi., det. Fischer", "Glaube nicht dass dieser Ex. die Type von *Mesotages decoris* sein kann. Foerster schreibt ausdrücklich dass *Mesotages* keine bogenförmige gekrümmten Fürchen an den 2. Tergit hat, Fischer, 1963". As pointed out above, I disagree with Fischer's statement and synonymize *Gnampydon bachmaieri* Fischer, 1957, with

*Gnaptodon decoris* (Foerster, 1862) comb. nov. There is a second specimen under *decoris* in the Foerster Collection, which does not belong to the type-series, and also has a reduced, easily overlooked transverse elevation on the 2nd tergite.

### *Gnaptodon erasmi* spec. nov. (figs. 103—111)

Holotype, ♀, length of body 1.6 mm, of fore wing 1.5 mm.

Head. — Antennal segments 18, length of 3rd segment 1.1 times 4th segment, length of 3rd and 4th segments 3.5 and 3.2 times their width, respectively, penultimate segment 1.9 times its width (fig. 105); length of maxillary palp 0.7 times height of head; length of eye twice temple in dorsal view (fig. 108); POL : Ø ocellus : OOL = 6 : 4 : 9; frons slightly convex, coriaceous; vertex completely coriaceous; face largely smooth, only laterally coriaceous, rather flat (fig. 111); length of malar space 1.7 times basal width of mandible.

Mesosoma. — Length of mesosoma 1.4 times its height; medio-longitudinal groove of mesocutum absent, represented only by a wide shallow depression (fig. 107); scutellar sulcus very shallow, narrowly crenulate (fig. 107); episternal scrobe rather shallow (fig. 103).

Wings. — Fore wing: r : 3-SR : SR1 = 7 : 10 : 46; 1-CU1 : 2-CU1 = 2 : 15; 2-SR : 3-SR : r-m = 11 : 5 : 8; length of pterostigma twice length of vein 1-R1; distance between wing apex and apex of marginal cell 1.9 times vein 1-R1; vein SR1 slightly curved (fig. 104).

Legs. — Length of femur, tibia and basitarsus of hind leg 3.2, 6.8 and 4.5 times their width, respectively.

Metasoma. — Length of 1st tergite 0.9 times its apical width, its surface coriaceous, and posteriorly rugulose (fig. 110); dorsal carinae distinct in basal 0.6 of 1st tergite; basal elevation of 2nd tergite distinct medio-posteriorly (fig. 110), its medial length 0.3 times rest of tergite; metasoma behind elevation of 2nd tergite largely coriaceous (fig. 103); 2nd suture deep, finely crenulate and rather evenly curved (fig. 110); medial length of 3rd tergite 0.7 times length of 2nd tergite; length of ovipositor sheath 0.07 times fore wing.

Colour. — Black; 4 basal segments of antenna (rest dark brown), palpi, tegulae and legs, brownish-yellow; 1st and 2nd tergite, and antero-lateral corners of 3rd tergite, reddish-brown; pterostigma light brown.

Holotype in Haeselbarth Collection: "Riva s. Garda (North Italy), 150 m, G/10.9.67, Haeselb."; (G = collected in vegetation of *Quercus ilex*-shrubwoodland, on lime, with very strong dominance of *Q. ilex*, mixed with *Fraxinus ornus*). Paratype, 1 ♂ (Rijksmuseum van Natuurlijke Historie, Leiden): "Ectoedemia groschkei (Skala) in *Vitex agnus-castus*, VU no. 80675 KE", "Ellas (Greece), Sept. 1980, S. B. J. Menken & E. J. v. Nieukerken", "4 km SW Padádées (Préveza), cult. area, roadside, 100 m, 39.17N-20.46 E, 25.ix.1980, st. 53"; antennal segments 19, basal elevation of 2nd tergite obsolete medially, otherwise as holotype.

Host: "Ectoedemia" groschkei (Skala) in *Vitex agnus-castus* L.

Note. It is a pleasure to me to dedicate this species to Dr. E. Haeselbarth (München).

### *Gnaptodon georginae* spec. nov.

(figs. 44—54)

Holotype, ♂, length of body 1.5 mm, of fore wing 1.4 mm.

Head. — Antennal segments 20, length of 3rd segment 1.1 times 4th segment, length of 3rd and 4th segments 3 and 2.7 times their width, respectively, penultimate segment 1.8 times its width (fig. 48); length of maxillary palp 0.7 times height of head; length of eye twice temple in dorsal view; POL : Ø ocellus : OOL = 7 : 5 : 10; frons flat, largely coriaceous; vertex distinctly coriaceous (fig. 52); face superficially coriaceous-pimply (fig. 45); length of malar space 1.3 times basal width of mandible.

Mesosoma. — Length of mesosoma 1.3 times its height; medio-longitudinal groove obsolete (fig. 49); scutellar sulcus narrow, rather shallow (fig. 49); episternal scrobe indistinct (fig. 44).

Wing. — Fore wing: r : 3-SR : SR1 = 5 : 9 : 60; 1-CU1 : 2-CU1 = 3 : 23; 2-SR : 3-SR : r-m = 24 : 9 : 15; length of pterostigma 1.9 times vein 1-R1; distance between wing apex and apex of marginal cell 1.8 times vein 1-R1; vein SR1 slightly sinuate (fig. 46).

Legs. — Length of femur, tibia, and basitarsus of hind leg 3.4, 7.7 and 5 times their width, respectively.

Metasoma. — Length of 1st tergite 0.8 times its apical width, its surface smooth; dorsal carinae distinct in basal 0.7 of 1st tergite (fig. 51); basal elevation of 2nd tergite distinctly narrowed laterally, medio-posteriorly distinctly curved (fig. 51), its medial length 0.8 times rest of tergite; area directly behind elevation of 2nd

tergite, as rest of tergites basally, weakly coriaceous (fig. 44); tergites otherwise smooth; 2nd suture rather deep, smooth; 3rd tergite with no antero-lateral grooves; medial length of 3rd tergite 0.9 times length of 3nd tergite (fig. 51).

Colour. — Black; tegulae (largely), pterostigma, 1st tergite medially, and antenna, dark brown; palpi, rest of 1st tergite, 2nd and 3rd tergites, antero-lateral corners of 3rd tergite, and legs (except the infuscated apex of hind tibia and the hind tarsus), brownish-yellow.

Holotype in Rijksmuseum van Natuurlijke Historie, Leiden: "ex *Stigmella hybnerella* (Hbn.), *Crataegus monogyna*, VU no. 80061 K1" "11 km ESE of Morris O.m., 26.iv.1980, Marsh & *Pistacia carr.*", "Stat. 19", "Algeria, E. v. Nieukerken, G. Bryan & P. Oosterbroek". Paratypes, 5 ♀ + 2 ♂: 1 ♀ + 1 ♂ (Museum Budapest): "Tahi, Pilis hegys." "1973.v.28, Szöcs J.", "*Nepticula malella* Stt. det. J. Szöcs", "*Malus sylvestris*"; 2 ♀ (Shaw Collection, Edinburgh): "Sulzchopf, BL., Switz(erland), LT/96, 470 m, H: *Stigmella tityrella*, mine coll. 11.10.76, PIE 23.7.77, S.E. Whitebread"; 1 ♀ (Zaykov Collection, Plovdiv): "22.9.1968, Rodopi, Parvez, leg. A. Germanov"; 1 ♂ (id): "21.5.1968, Plovdivsko Starosel, leg. A. Germanov"; 1 ♀ (Rijksmuseum van Natuurlijke Historie, Leiden): "Jambol, Ormana, 1981.v.27, leg. Zaykov". The latter 3 specimens are from Bulgaria.

Variation. — Antennal segments 19—21 (♀) or 20—23 (♂); 4—6 basal segments of ♀ antenna yellowish, penultimate segment twice its width (fig. 54), ♂ has basal antennal segments infuscated or blackish; length of fore wing 1.4 mm (3 specimens); length of pterostigma 1.2—1.9 times vein 1-R1; distance between apex of fore wing and apex of marginal cell 1.1—1.8 times vein 1-R1; medial length of basal elevation of 2nd tergite 0.6—1.0 times rest of tergite; 2nd tergite often completely smooth (fig. 53); 2nd and 3rd tergites usually yellowish, if dark brown then apical half of metasoma yellowish (ex *S. tityrella*); length of ovipositor sheath 0.04 times fore wing.

Hosts: *Stigmella hybnerella* (Hübner) in *Crataegus monogyna* L., *S. malella* (Stainton) in *Malus sylvestris* (L.), *S. ruficapitella* (Haworth) in *Quercus*, and *S. tityrella* (Stainton) in *Fagus sylvatica* L.

It is a great pleasure to me to dedicate this species to Dr. Georgina Bryan (Amsterdam), who made an important collection of reared parasites of Nepticulidae available for study.

**Gnaptodon nepalicus** Fischer

Fischer, 1966: 159—161, figs. 96—97. Shenefelt, 1975: 1124.

Fischer considered *G. nepalicus* an Oriental species; however, I prefer to include it among the Palaearctic spp., because it was collected at 6800 ft. in the Himalayas. The fauna at such high altitudes is more closely correlated with the (South) Palaearctic region than with the Oriental region. As shown in the foregoing key *nepalicus* is close to *G. pumilio* and seems to differ mainly in the colour of the antenna and in the wing venation.

**Gnaptodon nieukerkeni** spec. nov.  
(figs. 82—90)

Holotype, ♀, length of body and of fore wing 1.4 mm.

**Head.** — Antennal segments 18 (right antenna) or 19 (left one), length of 3rd segment 1.1 times 4th segment, length of 3rd and 4th segments 3.2 and 3.0 times their width, respectively, penultimate segment 2.2 times its width (fig. 89); length of maxillary palp 0.7 times height of head; length of eye 2.1 times temple in dorsal view (fig. 83); POL : Ø ocellus : OOL = 14 : 7 : 18; frons coriaceous, flat; vertex completely coriaceous; face rather convex and obliquely, finely rugulose-coriaceous, medially narrowly smooth (fig. 90); length of malar space 1.7 times basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.4 times its height; medio-longitudinal groove obsolete (fig. 87); scutellar sulcus deep, rather narrow, and distinctly crenulate (fig. 87); episternal scrobe absent.

**Wings.** — Fore wing: r : 3-SR : SR1 = 2 : 5 : 24; 1-CU1 : 2-CU1 = 1 : 10; 2-SR : 3-SR : r-m = 8 : 5 : 6; length of pterostigma 2.1 times vein 1-R1; distance between wing apex and apex of marginal cell 2.2 times vein 1-R1; vein SR1 slightly sinuate (fig. 84).

**Legs.** — Length of femur, tibia and basitarsus of hind leg 3.4, 7.3 and 5.0 times their width, respectively.

**Metasoma.** — Length of 1st tergite 0.8 times its apical width, its surface smooth (fig. 85); dorsal carinae present in basal third of 1st tergite; basal elevation of 2nd tergite distinct, its medial length 0.4 times medial length of rest of tergite; 2nd tergite behind elevation and rest of metasoma largely coriaceous; 2nd suture deep and smooth; 3rd tergite with no antero-lateral grooves and its medial length 1.2 times medial

length of 2nd tergite (fig. 85); length of ovipositor sheath 0.03 times fore wing.

**Colour.** — Black; antenna (except yellowish annellus), tegulae, pterostigma and wing veins, dark brown; palpi, and legs, yellowish (but hind coxa dorsally largely, hind femur apico-dorsally and hind tarsus (other tarsi slightly) infuscated; 2nd tergite medially and antero-laterally brown, rest of tergite dark brown).

Holotype in Rijksmuseum van Natuurlijke Historie, Leiden: "Parnassós Oros, 2 km, W. Summit (Voiotia), rocks, dwarf shrub, 38.32 N-22.35 E, 2000 m, 28.ix.1980, St. 58", "No. 80.685 KE, 21/24.x.80, in leaf-litter!", "ex *Stigmella cf. rhamnophila* (Amsel), *Rhamnus saxatilis*, VU no. 80.685 K.", "Ellas, Greece, September 1980, S. B. J. Menken, E. J. van Niekerken". Paratypes: 12 ♀ and 2 ♂ from same series (Vrije Universiteit, Amsterdam; Rijksmuseum van Natuurlijke Historie, Leiden; Museum Budapest; Collectie Zaykov, Plovdiv).

**Variation.** — Antennal segments 17—20; length of fore wing 1.2—1.4 mm; vein SR1 of fore wing usually more curved than in fig. 84; length of pterostigma 1.8—2.3 times vein 1-R1; distance between apex of fore wing and apex of marginal cell 1.9—2.4 times vein 1-R1; medial length of 3rd tergite 1.1—1.3 (♀) or 0.9 (♂) times medial length of 2nd tergite; 2nd tergite often (rather dark) brownish medially.

**Host:** *Stigmella cf. rhamnophila* (Amsel) in *Rhamnus saxatilis* Jacq.

**Gnaptodon pilosus** spec. nov.  
(figs. 73—81)

Holotype, ♀, length of body 1.4 mm, of fore wing 1.3 mm.

**Head.** — Antennal segments 21, length of 3rd segment 1.3 times 4th segment, length of 3rd and 4th segments 2.2 and 1.7 times their width, respectively, penultimate segment 1.4 times its width (fig. 75); length of maxillary palp 0.8 times height of head; length of eye 2.2 times temple in dorsal view (fig. 77); POL : Ø ocellus : OOL = 7 : 4 : 11; frons slightly concave behind antennal sockets, coriaceous; vertex distinctly coriaceous (fig. 77); face rather convex and largely smooth, only microsculptured laterally (fig. 76); long and densely setose between antennal sockets (figs. 76, 77; this setosity is absent in all other spp. treated in this paper); length of malar space 1.1 times basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.1 times its height; medio-longitudinal groove rather

deep, similar to notaui anteriorly (fig. 81); scutellar sulcus rather wide and deep, narrowly crenulate (fig. 81); episternal scrobe indistinct (fig. 73).

**Wings.** — Fore wing:  $r : 3\text{-SR} : \text{SR1} = 5 : 9 : 61$ ;  $1\text{-CU1} : 2\text{-CU1} = 1 : 8$ ;  $2\text{-SR} : 3\text{-SR} : r\text{-m} = 20 : 9 : 11$ ; length of pterostigma 1.8 times vein 1-R1; distance between wing apex and apex of marginal cell 1.8 times vein 1-R1; vein SR1 straight (fig. 74).

**Legs.** — Length of femur, tibia, and basitarsus of hind leg 3.4, 6.4 and 4 times their width, respectively.

**Metasoma.** — Length of 1st tergite 0.8 times its apical width, its surface aciculate in posterior half, the rest smooth (fig. 80), dorsal carinae present in basal 0.7; basal elevation of 2nd tergite distinct (somewhat cariniform at posterior edge), its medio-longitudinal length half the length of rest of 2nd tergite; metasoma behind elevation of 2nd tergite largely coriaceous (fig. 80); medio-longitudinal length of 2nd tergite equal to length of 3rd tergite; 2nd suture finely crenulate and rather deep; length of ovipositor sheath 0.08 times fore wing.

**Colour.** — Black; 4 basal segments of antenna (but scapus and pedicellus dark dorsally), palpi, humeral plate (tegula dark brown), legs (except dark brown tarsi), metasoma ventrally, 1st tergite (medially infuscated) and anterior half of 2nd tergite, yellowish; rest of antenna medially brown, its apical half dark brown; pronotal sides and mesopleuron with brownish stripe ventrally (absent in paratypes); apex of pterostigma whitish, rest dark brown.

Holotype in Museum Budapest: "Budapest, Rupphegy", "1974.vi.9, Szöcs J.", "*Quercus pubescens*, semen", "ex *Nepticula* sp., 1974.vii.8." Paratypes, 1 ♀ + 1 ♂ : 1 ♂ (Museum Budapest): "Hungaria, Budaörs. Naphegy", "1977.v.26., Szöcs J.", "*Quercus pubescens*", "ex *Nepticula eberhardi* Joh., det. J. Szöcs". As holotype, but metasoma slender, antennal segments 23, 1st tergite smooth, and pterostigma completely dark brown; 1 ♀ (Rijksmuseum van Natuurlijke Historie, Leiden): "Fót (= Hungary), 1960.ix.19", "lg. Mihályi". Antennal segments 21; as holotype, but medial length of 2nd tergite 1.1 times 3rd tergite.

Host: *Stigmella eberhardi* (Joh.) in *Quercus pubescens* Willd.

**Variation.** — Antennal segments 21—23, length of fore wing 1.3—1.5 mm; length of pterostigma 1.5—2.1 times vein 1-R1; distance between apex of fore wing and apex of marginal

cell 1.6—2.1 times vein 1-R1.

Note. *G. pilosus* resembles the Nearctic *G. glaber* Fischer, 1965, but *glaber* has the pterostigma yellowish, length of mesosoma about 1.5 times its height, 1st tergite longer than apical width, metasoma completely smooth and face distinctly coriaceous.

### **Gnaptodon pumilio (Nees)**

(figs. 22—33)

*Bracon pumilio* Nees, 1834: 90—91.

*Gnaptodon pumilio*; Fischer, 1972: 572—574, figs. 436—437. Shenefelt, 1975: 1124. Tobias, 1976b: 48. Van Achterberg, 1976: 60, figs. 37, 38. Huddleston, 1978: 47. Fischer, 1980: 202.

*Gnampydon pumilio*; Shaw & Askew, 1976: 131.

*Diraphus pygmaeus* Wesmael, 1838: 90, figs. 11, F.

A neotype of *Bracon pumilio* Nees, 1834, is here selected, because the original type-series is lost, it is the type-species of the genus *Gnaptodon* Haliday, 1837, and closely related species occur in the same faunal region. The hind coxae of the neotype are infuscated contrary to the original description, but Nees probably overlooked this feature.

Description of neotype, ♀, length of body and of fore wing 1.9 mm.

**Head.** — Antennal segments 21, length of 3rd segment 1.3 times 4th segment, length of 3rd and 4th segments 4.3 and 3.0 times their width, respectively, the penultimate segment 1.8 times its width; length of maxillary palp equal to height of head; eyes slightly emarginate (fig. 32); length of eye 2.6 times temple in dorsal view;  $\text{POL} : \emptyset \text{ ocellus} : \text{OOL} = 12 : 7 : 18$ ; frons flat, coriaceous; vertex largely smooth, convex; face rather convex (more so than in *decoris*) and laterally distinctly coriaceous (fig. 32); length of malar space 1.4 times basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.5 times its height; middle lobe of mesoscutum anteromedially slightly depressed (fig. 26); scutellar sulcus narrow, merely crenulate (fig. 26); medial carina of propodeum absent.

**Wings.** — Fore wing:  $r : 3\text{-SR} : \text{SR1} = 4 : 7 : 36$ ;  $1\text{-CU1} : 2\text{-CU1} = 5 : 31$ ;  $2\text{-SR} : 3\text{-SR} : r\text{-m} = 27 : 14 : 15$ ; distance of wing apex to apex of marginal cell 0.3 times vein 1-R1; length of pterostigma 1.1 times vein 1-R1 (fig. 24); vein SR1 straight (fig. 24).

**Legs.** — Length of femur, tibia, and basitarsus of hind leg 3.8, 9.2 and 7.5 times their width, respectively.

**Metasoma.** — Length of 1st tergite equal to

its apical width, its surface behind the spiracles finely rugulose and in front of the spiracles largely smooth (fig. 31); dorsal carinae of the 1st tergite present in basal half of tergite; posterior margin of transverse elevation of 2nd tergite straight medio-posteriorly, behind it rugulose; medial length of elevation of 2nd tergite 0.6 times medial length of rest of tergite; 2nd tergite with some punctures, its medial length 1.5 times medial length of 3rd tergite (fig. 31); 2nd inter-segmental suture medially deep and laterally obliterated, with a pair of obsolete, posteriorly diverging submedial grooves antero-laterally and a pair of obsolete grooves close to suture; ovipositor straight, without notch, and with a dorso-subapical nodus and some minute ventral teeth (fig. 30); length of ovipositor sheath 0.11 times fore wing.

**Colour.** — Black; mouthparts (including palpi), 3 basal antennal segments, tegulae, vein C + SC + R of fore wing, legs (but hind coxa largely infuscated) and metasoma ventrally, more or less yellowish-brown; pterostigma and 4th antennal segment dark brown; metasoma behind 1st tergite dorsally blackish-brown; wing membrane hyaline.

Neotype in Rijksmuseum van Natuurlijke Historie, Leiden: "Nederland, Wijster (Dr.), opposite Biol. Stat., 18—25.vi.1976, C. v. Achterberg".

Note. *Gnaptodon pumilio* (Nees) differs from *decoris*, in addition to the characters given in the key, by the distinctly setose back of the head (above the hypostomal carina) and the more convex face.

The type-series of *Diraphus pygmaeus* Wesmael, 1838, consists of one typical female specimen of *G. pumilio* (Nees) with the 2nd and 3rd tergites brownish, one female with yellowish 2nd and 3rd tergites ("var. 1" of Wesmael) and one male (probably not conspecific). The first specimen mentioned is here designated as lectotype. The lectotype has no distinct antero-lateral grooves at the 3rd tergite, the whole 1st tergite is dark brown, the 2nd metasomal suture is rather deep but smooth, the vertex is coriaceous, the 2nd tergite is distinctly sculptured and the hind coxae are yellowish.

**Variation.** — The variation within *pumilio* as interpreted in this paper is considerable. I have tried to split up the complex, but the results were unsatisfactory. The variation (especially of coloration) within a reared series is so extensive that any attempted division has been frustrated. Considering the available data, it is likely that

the specialisation within the complex has not resulted (yet) in recognizable species.

At least three forms can be discerned, of which form A seems to be ecologically differentiated from both other forms because it has been reared from Nepticulidae in herbs and bramble (*Rubus* spp.). The other forms have been reared from Nepticulidae in trees. I mention these three forms only to indicate the main lines of variations encountered. All characters mentioned are very variable, even within the same reared series.

Form A (including *pygmaeus* var. 1 (Wesmael)) has the 1st and 2nd tergites yellowish, with the middle of the 1st tergite usually dark brown, but sometimes the whole metasoma (except 1st tergite) is yellowish; vertex behind stemmaticum coriaceous; 2nd suture of metasoma shallow; antero-lateral grooves of 3rd tergite absent; hind coxa yellowish.

Form B has basal half of metasoma blackish or yellowish; vertex behind stemmaticum often smooth; 2nd suture of metasoma deep and crenulate; antero-lateral grooves of 3rd tergite deep and often finely crenulate; exceptionally the 3rd tergite has a separate crenulate and curved groove, directly behind 2nd suture instead of antero-lateral grooves (this indicates that these grooves may be the result of an amalgamation of the groove and the 2nd suture in the middle of the tergite); hind coxa yellowish or infuscated. Even within series from the same host there is considerable variation. The typical form has the whole metasoma blackish-brown; vertex behind stemmaticum smooth; 2nd suture of metasoma deep and smooth (fig. 31); antero-lateral grooves of 3rd tergite incomplete, shallow and smooth; hind coxa infuscated or yellowish. Intermediates to form B occur frequently, e.g. in a series from North Italy (St. Peter, Ahrntal, 1270 m, Haeselbarth Collection).

Specimens examined: 52 ♀ and 22 ♂ (of which 7 ♀ and 4 ♂ belong to form A). Antennal segments 19—23 (of both sexes mostly 21 or 22); length of body 1.6—1.8 mm; length of fore wing 1.7—1.9 mm; 4th antennal segment yellowish, exceptionally dark brown; area behind transverse elevation of 2nd tergite smooth to rather extensively rugulose; apex of metasoma frequently reddish brown; length of pterostigma: vein 1-R1 of fore wing : distance between wing apex and apex of marginal cell of fore wing = 0.8—1.2 : 1 : 0.25—0.6. The examined specimens originate from Norway, Sweden, Great Britain (Scotland, England), Ireland,

Netherlands (Bemelen (Bemelerberg); Cadier (Schietersberg); Castricum (dunes); 's Graveland (Ankeveense Plassen); Grevenbicht; Hilversum (heath Spanderswoud); Hulshorst (Leuvenumse Bos); Nederhorst den Berg (Spiegelpolder); Waarder; Wijster; Winterswijk), France, Italy, Austria, Hungary, Bulgaria and Greece.

Hosts: Reared from Nepticulidae in trees (form B and typical form):

in *Betula verrucosa* Ehrh.: (= *pendula* auct.)

ex *Stigmella luteella* (Stainton); U.K., Danbury, and Debden, both Essex.

in *Betula* spec.:

ex *S. betulincola* (Stainton); U.K., Thorpeness, Suffolk.

ex *S. confusella* (Wood); Norway, Åndalsnes, Møre & Romsd.

ex *S. continuella* (Stainton); Netherlands, Hilversum, heath.

ex *S. lapponica* (Wocke); Netherlands, dunes of Castricum; U.K., Delamere, Cheshire.

in *Salix caprea* L.:

ex *S. salicis* (Stainton); U.K., Benenden, Kent, (intermediate between form A and typical form, apex of metasoma partly yellowish).

in *Tilia* spec.:

ex *S. tiliae* (Frey); Hungary, Vásárosbée.

in *Ulmus procera* Salisbury:

ex *S. ulmivora* (Folome); U.K., Hallow, Worcestershire.

in *U. glabra* Mill.:

ex Nepticulidae; Hungary, Bátorliget.

in *Ostrya carpinifolia* Scopoli:

ex *S. carpinella* (Heinemann); Greece, Oíti Oros, Fthiotis, 4 km E, pávliani, 850 m.

in *Sorbus aucuparia* L.:

ex *S. magdalena* (Klimesch); Norway, Støren, Sør-Trøndelag, 60 m.

ex *S. sorbi* (Stainton); U.K., Blackford Hill, Edinburgh.

ex *S. spec.*; Ireland, Ballinhinch, Co. Galway.

in *Malus domestica* L.:

ex *S. malella* (Stainton); Netherlands, Grevenbicht (one ♂ has 2nd tergite yellowish, the other dark brown!).

ex *S. pomella* (Vaughan); Netherlands, Winterswijk.

in *Rhamnus catharticus* L.:

ex *S. rhamnella* (H.-S.); Hungary, Budaörs.

in *Quercus robur* L.:

ex *S. ruficapitella*-group; Netherlands, Hulshorst, Leuvenumse Bos; id., Hilversum,

heath; id., Bemelen, Bemelerberg.

ex *Ectoedemia caradjai* (Hering); France, Digne.

Form A:

in *Rubus fruticosus* agg.:

ex *Ectoedemia erythrogenella* (de Joannis); U.K., Benfleet, Essex.

ex *Stigmella splendidissimella* (H.-S.) or *aurella* (F.); Netherlands, Nederhorst den Berg, Spiegelpolder; id., 's Graveland, Ankeveense Plassen, (part of series has almost whole metasoma yellowish).

in *Rubus* spec.:

from same host(s); Netherlands, Hilversum. Spanderswoud, (whole metasoma (except middle of 1st tergite) yellowish).

in *Agrimonia eupatoria* L.:

ex *S. aeneofasciella* (H.-S.); Netherlands, Cadier, Schiepersberg (part of series has whole metasoma yellowish (♀) or behind 2nd tergite blackish (♂)); Austria, Schörfling, north of Attersee.

### *Gnaptodon ruficeps* spec. nov.

(figs. 94—102)

Holotype, ♀, length of body 1.6 mm, of fore wing 1.5 mm.

Head. — Antennal segments 21, length of 3rd segment 1.1 times 4th segment, length of 3rd and 4th segments 3.5 and 3 times their width, respectively, penultimate segment 1.8 times its width (fig. 95); length of maxillary palp 0.8 times height of head; length of eye 1.8 times temple in dorsal view (fig. 98); POL : Ø ocellus : OOL = 12 : 7 : 18; frons slightly convex, coriaceous; vertex completely coriaceous (fig. 98); face rather convex and largely coriaceous (fig. 101); length of malar space 2.1 times basal width of mandible.

Mesosoma. — Length of mesosoma 1.2 times its height; medio-longitudinal groove of mesoscutum absent, represented by only a wide, shallow low depression (fig. 100); scutellar sulcus rather wide and deep (fig. 100); episternal scrobe shallow.

Wings. — Fore wing: r : 3-SR : SR1 = 3 : 6 : 22; 1-CU1 : 2-CU1 = 1 : 8; 2-SR : 3-SR : r-m = 10 : 6 : 7; length of pterostigma 1.5 times vein 1-R1; distance between apex of fore wing and apex of marginal cell 1.6 times vein 1-R1; vein SR1 slightly curved (fig. 96).

Legs. — Length of femur, tibia and basitarsus of hind leg 3.9, 9 and 6 times their width, respectively.

Metasoma. — Length of 1st tergite 0.6 times its apical width, its surface superficially coriaceous; dorsal carinae present in basal half of 1st tergite (fig. 102); basal elevation of 2nd tergite indistinct, its medial length 0.5 times rest of tergite; 2nd tergite behind elevation and rest of metasoma largely coriaceous (fig. 94); 2nd suture deep, smooth and distinctly bent (fig. 102); 3rd tergite with no antero-lateral grooves; medial length of 3rd tergite 0.8 times medial length of 2nd tergite (fig. 102); length of ovipositor sheath 0.08 times fore wing.

Couleur. — Yellowish-brown; stemmaticum, antenna (but scapus largely yellowish), mesosoma (but propleuron, mesopleuron dorsally and metapleuron brownish), and pterostigma, dark brown; vertex (partly) and telotarsi, infuscated.

Holotype in Museum Budapest: "Nagykovácsi (= Hungary), 1967, vii.9, Szöcs J.", "ex *Nepticula dorycniella* Suijs", "*Dorycnium germanicum*".

Host: *Trifurcula dorycniella* (Suijs) in *Dorycnium germanicum* (Grenli).

#### Gnaptodon vlugi spec. nov. (figs. 64—72)

Holotype, ♂, length of body 1.2 mm, of fore wing 1.4 mm.

Head. — Antennal segments 18, antenna widened apically (fig. 64), length of 3rd segment 1.1 times 4th segment, length of 3rd and 4th segments 3.5 and 3.2 times their width, respectively, penultimate segment 2.2 times its width (fig. 66); length of maxillary palp 0.9 times height of head; length of eye 1.7 times temple in dorsal view (fig. 71); POL : Ø ocellus : OOL = 16 : 8 : 19; frons almost smooth, slightly depressed behind antennal sockets; vertex largely smooth; face largely smooth, laterally indistinctly micro-sculptured, rather convex (fig. 68); length of malar space equal to basal width of mandible.

Mesosoma. — Length of mesosoma 1.3 times its height; medio-longitudinal groove of mesoscutum shallow but distinct (fig. 69); scutellar sulcus rather wide, distinctly crenulate (fig. 69); episternal scrobe deep (fig. 64).

Wings. — Fore wing: r : 3-SR : SR1 = 6 : 11 : 54; 1-CU1 : 2-CU1 = 3 : 11; 2-SR : 3-SR : r-m = 24 : 11 : 16; length of pterostigma 1.9 times vein 1-R1; distance between apex of fore wing and apex of marginal cell 2.2 times vein 1-R1 (fig. 65); vein SR1 straight.

Legs. — Length of femur, tibia and basitarsus

of hind leg 3.6, 6.6 and 5.2 times their width, respectively.

Metasoma. — Length of 1st tergite 0.9 times its apical width, its surface smooth, and dorsal carinae obsolescent (fig. 72); basal elevation of 2nd tergite weakly differentiated, strongly transverse, its medial length 0.4 times medial length of rest of tergite (fig. 72); 2nd tergite behind elevation coriaceous but posteriorly smooth; medial length of 2nd tergite 1.2 times medial length of 3rd tergite; 3rd tergite smooth and with shallow and smooth antero-lateral grooves (fig. 72); 2nd suture deep, medially distinctly crenulate.

Colour. — Black; palpi, legs (except infuscated telotarsi), 5 basal segments of antenna, tegulae, 1st and 2nd tergites, antero-lateral corners of 3rd tergite and anterior half of metasoma ventrally, ivory-whitish; pterostigma brown; rest of antenna (dark) brown.

Holotype in Rijksmuseum van Natuurlijke Historie, Leiden: "Sweden, Hallandsl., Särö-Hamra, swept, 26.6.1977, leg. H. J. Vlug". It is a pleasure to me to dedicate this species to its collector, Mr. H. J. Vlug (Scherpenzeel).

#### THE ECOLOGY OF THE REARED PALAEARCTIC GNAPDOTON SPECIES

As shown in fig. 131, if reared more than once, the hosts of *Gnaptodon* species are usually found on plants of several families. Obviously the parasites do not select certain plant groups. If the host plants are arranged according to their morphology (trees, (low) shrubs, and (non-woody) herbs), however, the picture changes (fig. 130). The assignment of host plants of the Nepticulidae to a tree, shrub, or herb zone is, of course rough: the low shoots of a tree may be lower than a large herb, and the same applies for a dwarf shrub. Nevertheless, the species seem to select for a certain vegetation zone; if more than one zone is included (e.g. *pumilio*, no. 1 in fig. 130) then the specimens in another zone are aberrant in colour and/or morphology with respect to the nominate form (e.g. form A of *pumilio* in herbs) and may constitute already a good biological species or be in the process of active sympatric speciation.

If two morphologically very close species occur in the same zone (nos 3 and 5 in fig. 130) then one of the species is specialized: in this case no. 5 (*pilosus*) seems to be restricted to Nepticulidae in *Quercus*, while no. 3 (*georginae*) parasitizes Nepticulidae in other trees (and high

shrubs). In the case of *erasmi* (no. 6) and *nieuwerkerkeni* (no. 7), the latter seems to be restricted to dwarf shrubs among rocks at high altitude. *G. erasmi* is known from 100—150 m altitude and occurs in higher shrubwood.

Summarizing, the selection of a vegetation zone is of major importance. Within one zone closely related species are ecologically separated because of their preference to a certain host-plant (*pilosus* in *Quercus*, *georginae* in other trees) or to a certain altitude (*erasmi* at low altitude, *nieuwerkerkeni* at high altitude). Obviously a lot of research, especially cross-breeding experiments, still has to be done before definitive conclusions can be drawn.

## B. AFROTROPICAL REGION

### KEY TO AFROTROPICAL SPECIES OF THE GENUS *GNAPTODON* HALIDAY

1. Second tergite of metasoma with distinct transverse elevation basally (figs. 119, 128); length of vein SR1 of fore wing 7—10.5 times vein 3-SR (figs. 114, 122) ..... 2
- Second tergite with no distinct transverse elevation basally; length of vein SR1 of fore wing about 3 times vein 3-SR ..... *unifossa* Fischer
2. Distance between fore wing apex and apex of marginal cell about 0.7 times vein 1-R1 (metacarp); length of pterostigma about 1.1 times vein 1-R1; length of vein SR1 of fore wing about 10 times vein 3-SR (fig. 122); 1st tergite largely aciculate-rugulose (fig. 128); antenna comparatively slender basally (fig. 121) ..... *similis* spec. nov.
- Distance between fore wing apex and apex of marginal cell about 1.3 times vein 1-R1; length of pterostigma 1.5—1.9 times vein 1-R1; length of vein SR1 of fore wing 7—8 times vein 3-SR (fig. 114); 1st tergite largely smooth (fig. 119); antenna rather robust basally (fig. 112) ..... *bini* spec. nov.

### *Gnaptodon bini* spec. nov.

(figs. 112—120)

Holotype, ♀, length of body, and of fore wing 1.1 mm.

Head. — Antennal segments 14, length of 3rd segment 1.3 times 4th segment, length of 3rd and 4th segments 2.5 and 2.0 times their width, respectively, penultimate segment 1.8 times its width; length of maxillary palp 0.8 times height of head; length of eye 1.9 times temple in dorsal view, POL : Ø ocellus : OOL = 9 : 4 : 10;

fronts slightly impressed, coriaceous (figs. 116, 117); vertex coriaceous; face rather convex, laterally coriaceous, rest smooth (fig. 117); length of malar space 1.2 times basal width of mandible

Mesosoma. — Length of mesosoma 1.4 times its height; medio-longitudinal groove of mesoscutum absent; scutellar sulcus narrow (fig. 120); episternal scrobe obsolescent (fig. 112).

Wings. — Fore wing: r : 3-SR : 3-R1 = 5 : 10 : 68; 1-CU1 : 2-CU1 = 3 : 26; 2-SR : 3-SR : r-m = 25 : 10 : 11; length of pterostigma 1.9 times vein 1-R1; distance between wing apex and apex of marginal cell 1.4 times vein 1-R1; vein SR1 slightly curved.

Legs. — Length of femur, tibia and basitarsus of hind leg 3.2, 6.3 and 4 times their width, respectively.

Metasoma. — Length of 1st tergite 0.7 times its apical width, its surface smooth; dorsal carinae of 1st tergite obsolescent (fig. 119); basal elevation of 2nd tergite slightly developed medially, rest of 2nd tergite and 3rd tergite coriaceous, rest of metasoma largely transversely micro-aciculate (fig. 112); medial length of basal elevation of 2nd tergite 0.4 times rest of tergite; medial length of 2nd tergite 0.9 times length 3rd tergite (fig. 119); 2nd suture deep, smooth, 3rd tergite with no antero-lateral grooves; length of ovipositor sheath 0.08 times fore wing.

Colour. — Blackish or dark brown; clypeus ventrally, mandibles, 4 basal segments of antenna, tegula, legs (but fore and middle telotarsi and hind tarsus infuscated), and 3 basal segments of metasoma, brownish-yellow; rest of metasoma dark brown; humeral plate whitish; pterostigma dark brown; palpi whitish.

Holotype in Rijksmuseum van Natuurlijke Historie, Leiden: "Somalia, Afgoi, iv.1977. Lower Shabelli Valley, F. Bin". Additional material: 1 ♀ (non-type), in same institute, topotypic, length of fore wing 1 mm, antennal segments 16, robust antenna as holotype (length of 3rd and 4th segments 2.5 and 2 times their width, respectively), length of pterostigma 1.5 times vein 1-R1, distance between apex of fore wing and apex of marginal cell 1.3 times vein 1-R1; hind tarsus and whole metasoma yellowish; head (except stemmaticum) brownish-yellow; 1st tergite with some micro-aciculae. Not labelled as paratype because of aberrant coloration.

Note. The combination of the short distance between the apex of the fore wing and the apex of the marginal cell, the short vein 1-R1, and the

low number of antennal segments, differentiates it from the known Palaearctic species. The only Oriental species (described in this paper) differs e.g. by its slender pterostigma. I am pleased to dedicate this species to Dr. F. Bin (Perugia), who collected several interesting Braconidae in Somalia.

**Gnaptodon similis spec. nov.**

(figs. 121—129)

Holotype, ♀, length of body 1.2 mm, of fore wing 1.3 mm.

Head. — Antennal segments 17, length of 3rd segment 1.2 times 4th segment, length of 3rd and 4th segments 3 and 2.5 times their width, respectively, penultimate segment 2.3 times its width (fig. 123); length of maxillary palp 0.8 times height of head; length of eye 1.1 times temple in dorsal view; POL : Ø ocellus : OOL = 6 : 3 : 8; frons slightly impressed, coriaceous; vertex strongly shiny, coriaceous (fig. 124); face rugulo-coriaceous laterally, rest smooth, rather convex (fig. 125); length of malar space equal to basal width of mandible.

Mesosoma. — Length of mesosoma 1.4 times its height; medio-longitudinal groove of mesocutum absent (fig. 129); scutellar sulcus narrow, merely finely crenulate (fig. 129); episternal scrobe small and shallow.

Wings. — Fore wing: r : 3-SR : SR1 = 4 : 4 : 42; 1-CU1 : 2-CU1 = 1 : 11; 2-SR : 3-SR : r-m = 14 : 4 : 10; length of pterostigma 1.1 times vein 1-R1 (fig. 122); distance between wing apex and apex of marginal cell 0.7 times vein 1-R1; vein SR1 straight (fig. 122).

Legs. — Length of femur, tibia, and basitarsus of hind leg 3.6, 6.2 and 4.5 times their width, respectively.

Metasoma. — Length of 1st tergite equal to its apical width, its surface largely aciculate-rugulose (fig. 128); dorsal carinae distinct in basal half of 1st tergite; basal elevation of 2nd tergite distinct, posteriorly straight (fig. 128), its medial length 0.3 times length of rest of tergite; 2nd tergite medially and 3rd tergite basally coriaceous, rest of metasoma smooth (fig. 121); 2nd suture deep and smooth; medial length of 2nd tergite 1.1 times length of 3rd tergite; length of ovipositor sheath 0.08 times fore wing.

Colour. — Brownish-yellow; 6th—17th antennal segments, 3rd and 4th metasomal tergites, ovipositor sheath and stemmaticum, dark brown or blackish; mesosoma and rest of metasoma, brown; pterostigma rather light brown.

Holotype in British Museum (Natural Histo-

ry), London: "Port St. John(s), Pondoland, April 5—30, 1923", "S. Africa, R. E. Turner, Brit. Mus., 1923—286".

Note. Resembles the Palaearctic *G. decoris*, but *similis* has vein SR1 of fore wing straight, head and base of antenna yellowish, metasoma distinctly sculptured, and fewer antennal segments (20—23 in *decoris*).

**C. ORIENTAL REGION**

**Gnaptodon orientalis spec. nov.**

(figs. 34—43)

Holotype, ♀, length of body 1.0 mm, of fore wing 1.2 mm.

Head. — Antennal segments 19, length of 3rd segment 1.3 times 4th segment, length of 3rd and 4th segments 3.3 and 2.5 times their width, respectively; penultimate segment 2.3 times its width (fig. 41); length of maxillary palp 0.6 times height of head; length of eye 2.6 times temple in dorsal view; POL : Ø ocellus : OOL = 8 : 4 : 12; frons virtually flat and smooth; vertex convex and smooth; face rather convex and smooth; length of malar space 1.5 times basal width of mandible.

Mesosoma. — Length of mesosoma 1.2 times its height; mesoscutal lobes evenly setose, without medial depression (fig. 42); scutellar sulcus narrow and virtually smooth (fig. 42).

Wings. — Fore wing: r : 3-SR : SR1 = 3 : 4 : 41; 1-CU1 : 2-CU1 = 3 : 25; 2-SR : 3-SR : r-m = 11 : 4 : 8; length of pterostigma 1.4 times vein 1-R1; length of distance between apex of wing and apex of marginal cell 0.8 times vein 1-R1 (fig. 37); pterostigma slender (fig. 37; all other spp. treated in this paper have the pterostigma more robust (figs. 13, 20, 24)); vein SR1 slightly curved (fig. 37).

Legs. — Length of femur, tibia, and basitarsus of hind leg 3.5, 8.0, and 5.5 times their width, respectively.

Metasoma. — Length of 1st tergite equal to its apical width, its surface largely smooth, with dorsal carinae developed in basal two-thirds of tergite (fig. 43); curved transverse elevation of 2nd tergite distinct, in front smooth, behind it superficially coriaceous (fig. 43); 2nd intersegmental suture of metasoma medially distinct, smooth, with no additional grooves; setae rather sparse and spread; ovipositor straight, with nodus subapically (fig. 34); length of ovipositor sheath 0.05 times fore wing.

Colour. — Yellowish-brown; antenna (except scapus); stemmaticum, mesoscutum

largely, 3rd-5th tergites medially, ovipositor sheath, pterosigma, and vein 1-R1, dark brown; rest of veins brown; scutellum, medial part of metanotum, propodeum, and 1st tergite basally, hind tarsus and telotarsi, infuscated; wing membrane hyaline.

Holotype in Bernice P. Bishop Museum, Honolulu: "Thailand: Trang Prov., Khaophappha Khaochang, 200 m., 11–15.i.1964", "G. A. Samuelson, Malaise Trap, Bishop".

Note. — *G. orientalis* spec. nov. runs in my key to the Palaearctic species to *G. decoris* (Foerster); however, *orientalis* differs by the more slender pterostigma and longer marginal cell of the fore wing (fig. 37 versus fig. 20), the yellowish head and base of the metasoma, and by the (nearly) smooth face and 1st tergite (both more or less sculptured in *decoris*). Of the Afrotropical spp., it most resembles *G. similis* spec. nov. from S. Africa; however, *orientalis* differs by the slender pterostigma and marginal cell of fore wing (fig. 37 versus fig. 122) and by the smooth 1st tergite (fig. 43 versus fig. 128). It runs in the key to the Australian species of *Gnaptodon* by Fischer (1978: 397–398) to *G. novobritanicus* Fischer, 1971, because of the rather evenly setose mesoscutum. However, *G. novobritanicus* is not closely related; it has a longer ovipositor sheath (longer than half length of metasoma), longer maxillary palp (equal to height of head), more antennal segments (26 in holotype), different colour (mesosoma black), and is twice as large. Additionally *G. novobritanicus* has a weakly developed ventral part of the occipital carina and the propodeum has a medial carina.

#### PHYLOGENETIC RELATIONSHIPS

The Gnaptodontinae may be easily mistaken for a group of the Opiinae because of the absence of the prepectal carina, the almost flat and glabrous labrum, and the presence of a shallow hypoclypeal depression. However, the wing venation, the more or less developed transverse elevation of the 2nd metasomal tergite, the pit in front of the propodeal spiracle, and the 3-segmented labial palp of the Gnaptodontinae would be aberrant within the Opiinae. Also the biology is aberrant; Opiinae are obligatory larval endoparasites of Diptera, while the Gnaptodontinae (as far as known) are obligatory (endo)parasites of Nepticulidae (Lepidoptera).

The cephalic structures of the final instar larva of *Gnaptodon* are fairly complete and include robust and toothed mandibles (fig. 43 in Čapek,

1970). The mandibles of the larvae of Opiinae are slender and toothless. The toothed mandibles of the larvae of the Gnaptodontinae are peculiar (if it is a real endoparasite), because endoparasites such as Opiinae, Alysiinae and the endoparasitic groups, e.g. of the Rogadinae, have smooth mandibles. This may indicate that *Gnaptodon* actually is an ectoparasite, which glues the egg to the host's intersegmental membrane (as in the ectoparasitic *Rhysipolis*; Dr. M. R. Shaw, in litt.). A really sound and accurate proof that *Gnaptodon* is an endoparasite has not yet been obtained; it is only deduced from circumstantial evidence (e.g. the host remains look as though an endoparasite has been there and the parasitized host is mobile and able to spin a cocoon when it leaves the mine). The delicate cocoon of *Gnaptodon* is formed in the cocoon of the host.

The cephalic structures of the larvae of some ectoparasitic Rogadinae are similar to those of the Gnaptodontinae. However, he similarity is based on symplesiomorphous character-states (e.g., the toothed mandibles). The cephalic structures of the larvae of Gnaptodontinae are completely different from the more or less reduced cephalic structures of the larvae of Opiinae. Despite this evidence Fischer (1970, 1972 & 1977) and Tobias (1976a, not 1976b) favour the inclusion of the Gnaptodontinae as a tribe in the Opiinae, because, for example, the transverse elevation of the 2nd tergite is considered to be too aberrant an evolutionary tendency to include it in the Rogadinae (Fischer, 1972: 56) as proposed by Čapek (1970). Peculiarly, it is forgotten that this evolutionary tendency is also absent in the Opiinae. Fischer (1972: 56) provisionally retains his Gnaptodontini in the Opiinae because of "konventionellen Gründen".

Within the Rogadinae the Gnaptodontinae would fit in near the Exothecini. The synapomorphous character-states shared with the Exothecini are the absence of the prepectal carina and the precoxal sulcus, and the scarcely developed laterope. Unfortunately these are all reductions and such "negative apomorphous character-states" are comparatively less reliable for a phylogenetic arrangement than "positive apomorphous character-states", such as the peculiar curved transverse elevation of the 2nd tergite in the Gnaptodontinae. The only positive synapomorphy with the Exothecini is in the biology and then only in being parasites of leaf-miners.

The morphology of the Gnaptodontinae (as

far as I have examined the group) seems too derived to give any firm clue about its sister-group. An exception may be the rather flat labrum combined with the transverse, rather shallow hypoclypeal depression (figs. 6, 14), which is aberrant for (almost all of) the Rogadinae and normal for a large part of the Opiinae. The only alternative to its inclusion in the Rogadinae or in the Opiinae seems to be to consider it an old archaic subfamily, and the presence of rather numerous species both in the Australian and Palaearctic regions supports this view. Thus the Gnaptodontinae are considered to have branched off somewhere from the stem of group B (Van Achterberg, 1976, fig. 123), which includes the Opiinae and Alysiinae. All of the group B are now exclusively parasites of Diptera and originally endoparasites of mining larvae of Diptera (as the majority of the Opiinae still are). Later they switched to larvae in (more or less decaying) fruits, followed by accepting hosts in decaying vegetable matter (e.g. dung), and finally in decaying animal matter (carrion). It is interesting to note that the Gnaptodontinae are (still) specialized (?ecto)parasites of mining larvae of an archaic group of Lepidoptera; this makes it likely that the Gnaptodontinae branched off before the Opiinae became specialized on dipterous hosts (and if *Gnaptodon* is an ectoparasite, even before the development of endoparasitism), since the group from which the Gnaptodontinae, Opiinae and Alysiinae stem seems to consist of solitary ectoparasites of various orders, including Lepidoptera and Diptera, as still are found in the Rogadinae.

Another problem is the position of the group B within the Braconidae. Tobias (1967, fig. 43) placed it as a sister-group of the Helconinae, while Čapek (1970) and Van Achterberg (1976) considered the group a branch of the "cyclostome"-group, including the Rogadinae. The latter view has recently gained much support from the work of Edson & Vinson (1979) on the morphology of the venom apparatus of the female. The venom apparatus of the Opiinae and Alysiinae is similar to that of the Rogadinae and different from the venom apparatus of the Helconinae. Unfortunately the venom apparatus of the Gnaptodontinae remains still to be investigated; thus its similarity to that of the Opiinae remains to be proved.

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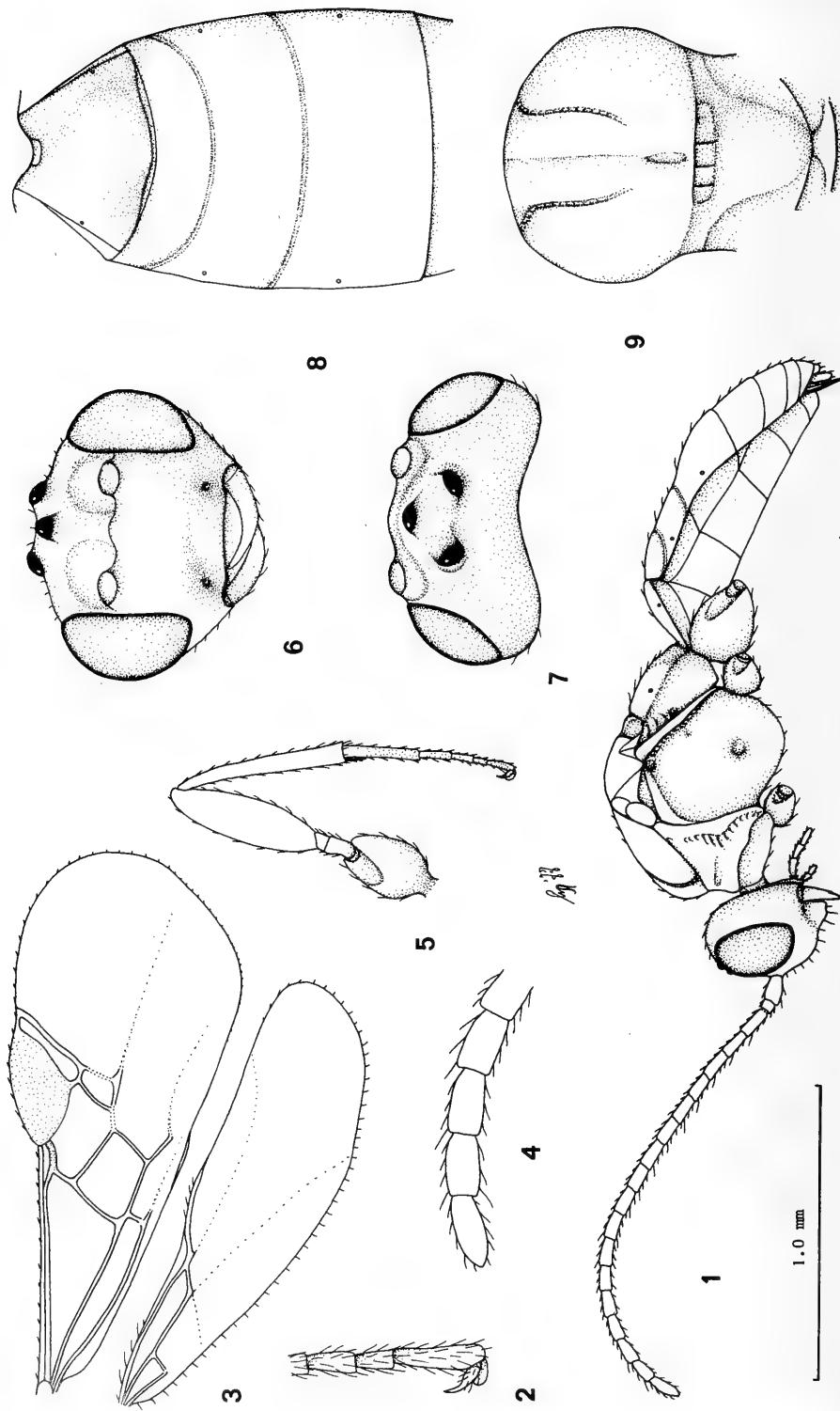
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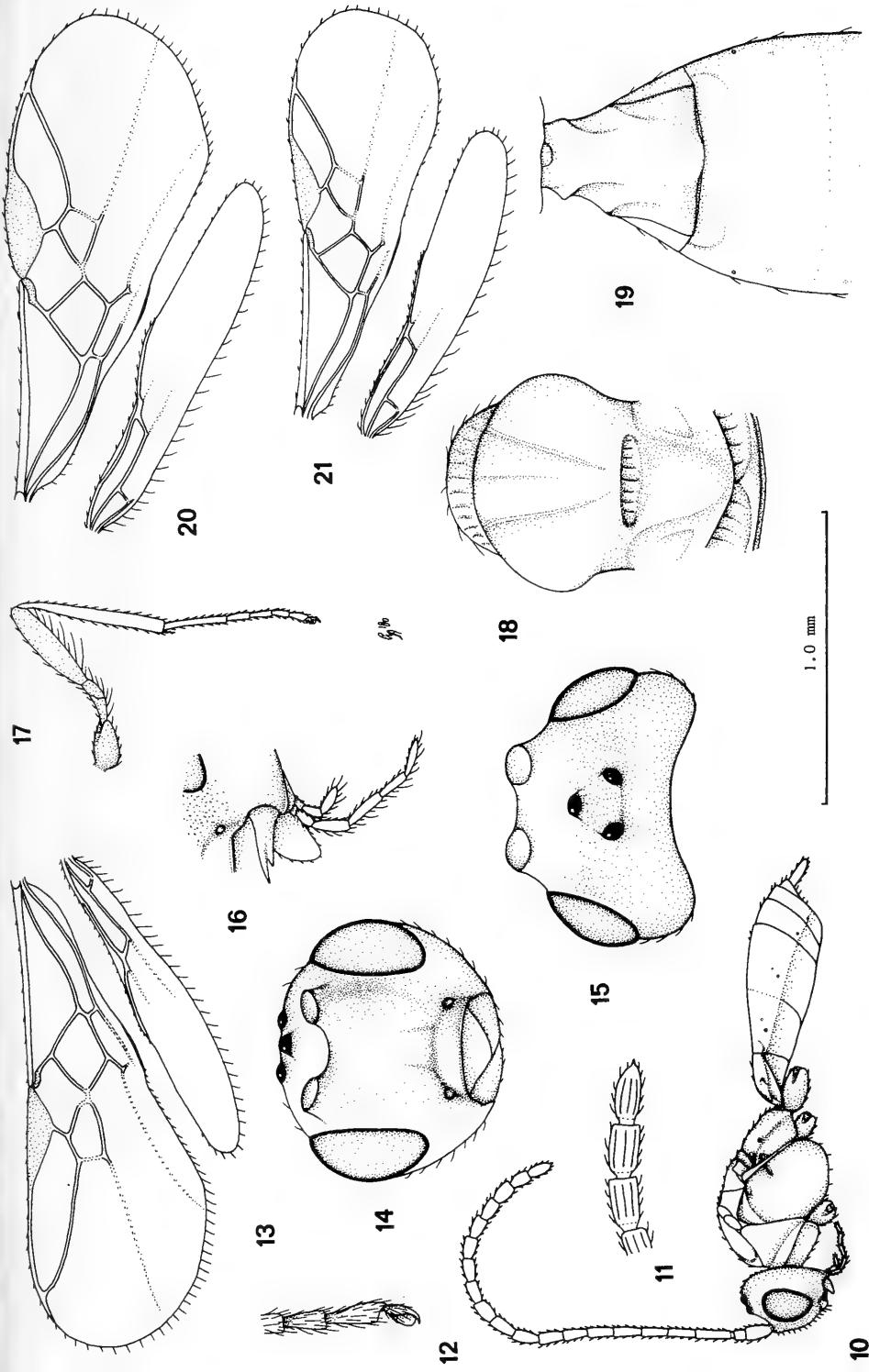
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CHECKLIST OF NAMES USED IN THE GENUS *GNAPTONDON* HALIDAY

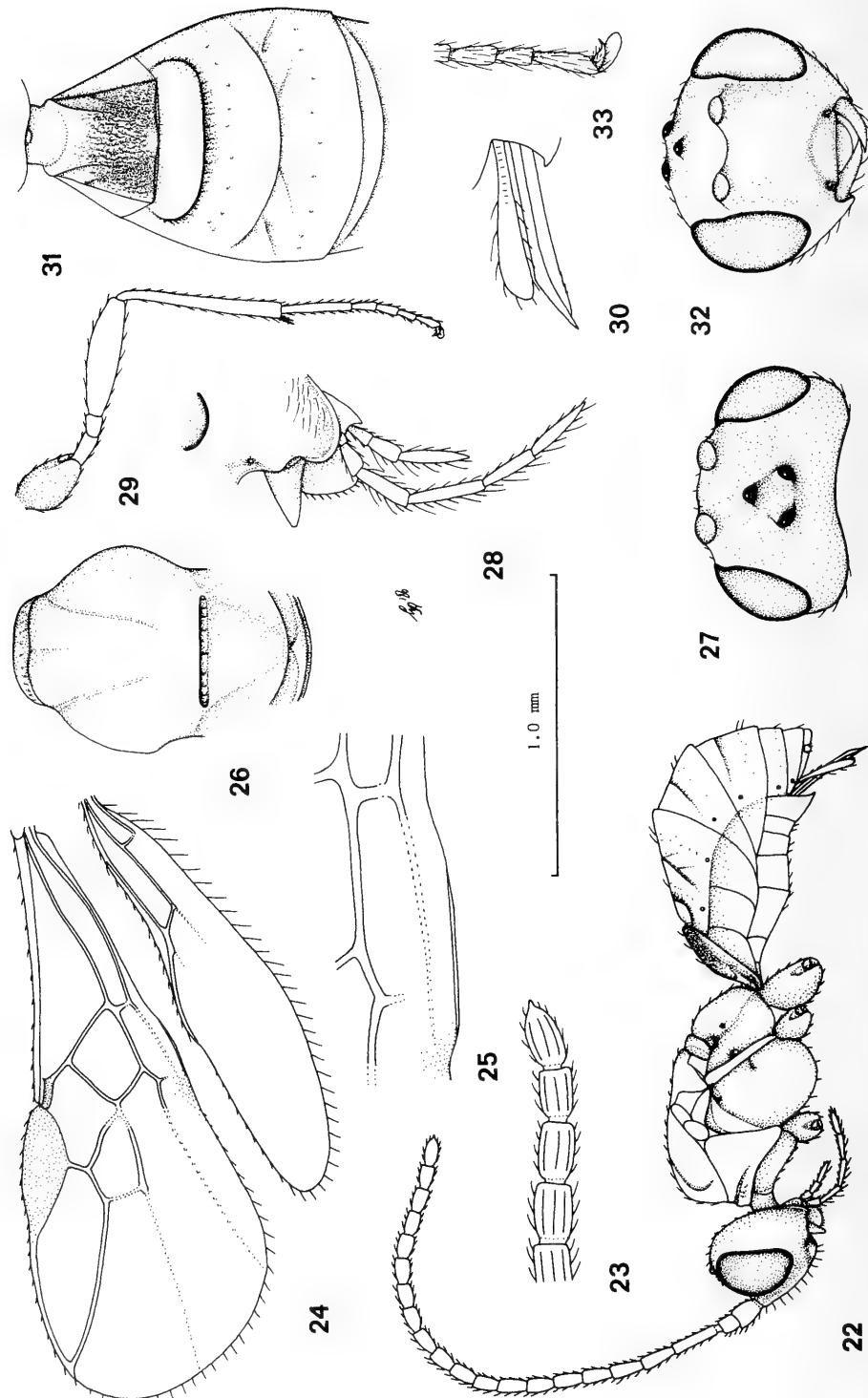
Name	Type-locality	page
<i>apheles</i> spec. nov.	North Italy . . . . .	29
<i>bachmaieri</i> (Fischer, 1957)	West Germany . . . . .	31
<i>bicolor</i> Fischer, 1965	U.S.A. (North Carolina) . . . . .	29
<i>bini</i> spec. nov.	Somalia . . . . .	39
<i>breviradialis</i> Fischer, 1959	Hungary . . . . .	30
<i>brevis</i> spec. nov.	Hungary . . . . .	30
<i>catamaranensis</i> Fischer, 1978	Tasmania . . . . .	—
<i>clarimacula</i> Fischer, 1978	Tasmania . . . . .	—
<i>decoris</i> (Foerster, 1862)	West Germany . . . . .	31
<i>dispar</i> Fischer, 1978	Tasmania . . . . .	—
<i>erasmi</i> spec. nov.	North Italy . . . . .	32
<i>georginae</i> spec. nov.	Algeria . . . . .	33
<i>glaber</i> Fischer, 1965	U.S.A. (Florida) . . . . .	29, 35
<i>klemensiewiczi</i> Niezabitowski, 1910	Poland . . . . .	31
<i>longicauda</i> Fischer, 1965	U.S.A. (Maryland) . . . . .	—
<i>nepalicus</i> Fischer, 1966	Nepal . . . . .	34
<i>nepticulae</i> (Rohwer, 1915)	U.S.A. (Virginia) . . . . .	29
<i>nieukerkeni</i> spec. nov.	Greece . . . . .	34
<i>novobritannicus</i> Fischer, 1978	Bismarck Archipelago . . . . .	41
<i>novoteutonicus</i> Fischer, 1967	Brazil . . . . .	29
<i>orientalis</i> spec. nov.	Thailand . . . . .	40
<i>pilosus</i> spec. nov.	Hungary . . . . .	34
<i>pulchrigaster</i> Fischer, 1965	U.S.A. (New York) . . . . .	29
<i>pumilio</i> (Nees, 1834)	Netherlands (neotype) . . . . .	35
<i>pygmaeus</i> (Wesmael, 1838)	Belgium . . . . .	35
<i>recticarinatus</i> Fischer, 1965	Canada (Yukon Terr.) . . . . .	—
<i>rotundincisus</i> Fischer, 1978	Tasmania . . . . .	—
<i>ruficeps</i> spec. nov.	Hungary . . . . .	37
<i>rugulosus</i> Fischer, 1965	U.S.A. (New York) . . . . .	—
<i>similis</i> spec. nov.	South Africa . . . . .	40
<i>sinuatus</i> Fischer, 1965	Canada (Yukon Terr.) . . . . .	—
<i>talamalausensis</i> Fischer, 1978	Bismarck Archipelago . . . . .	—
<i>tasmanicus</i> Fischer, 1978	Tasmania . . . . .	—
<i>tricrenulatus</i> Fischer, 1978	Tasmania . . . . .	—
<i>unifossa</i> Fischer, 1963	Tasmania . . . . .	—
<i>vlugi</i> spec. nov.	Sweden . . . . .	38



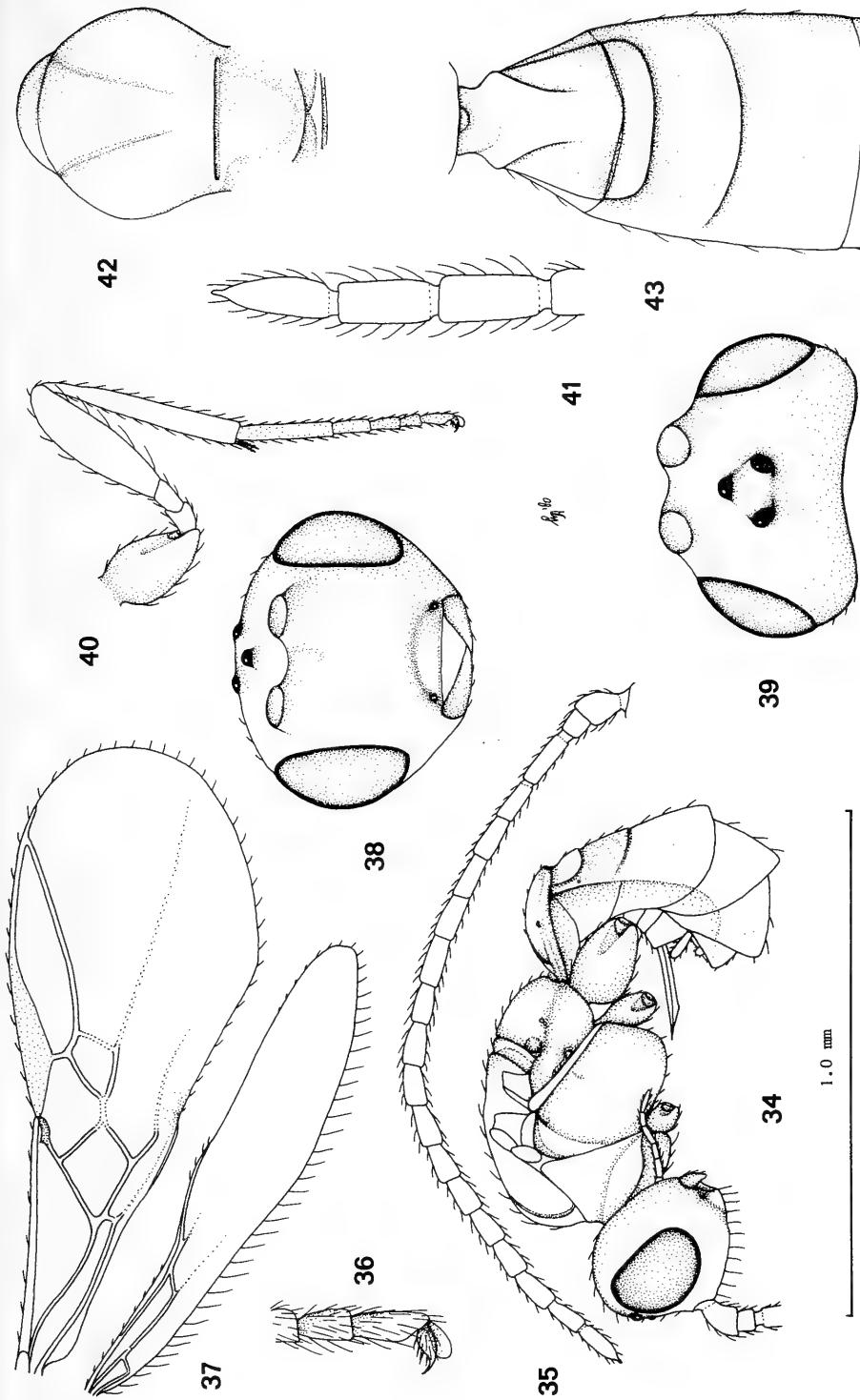
Figs. 1—9. *Gnatogaster mongolica* Tobias, paratype, ♀. 1; habitus, lateral aspect; 2; hind claw; 3; wings; 4; apex of antenna; 5; hind leg; 6; head, frontal aspect; 7; head, dorsal aspect; 8; 1st—3rd tergites, dorsal aspect; 9; meso- and metanotum, dorsal aspect. 1, 3, 5; scale-line, 1 ×; 2, 4, 2.5 ×; 6—9; 1.7 ×.



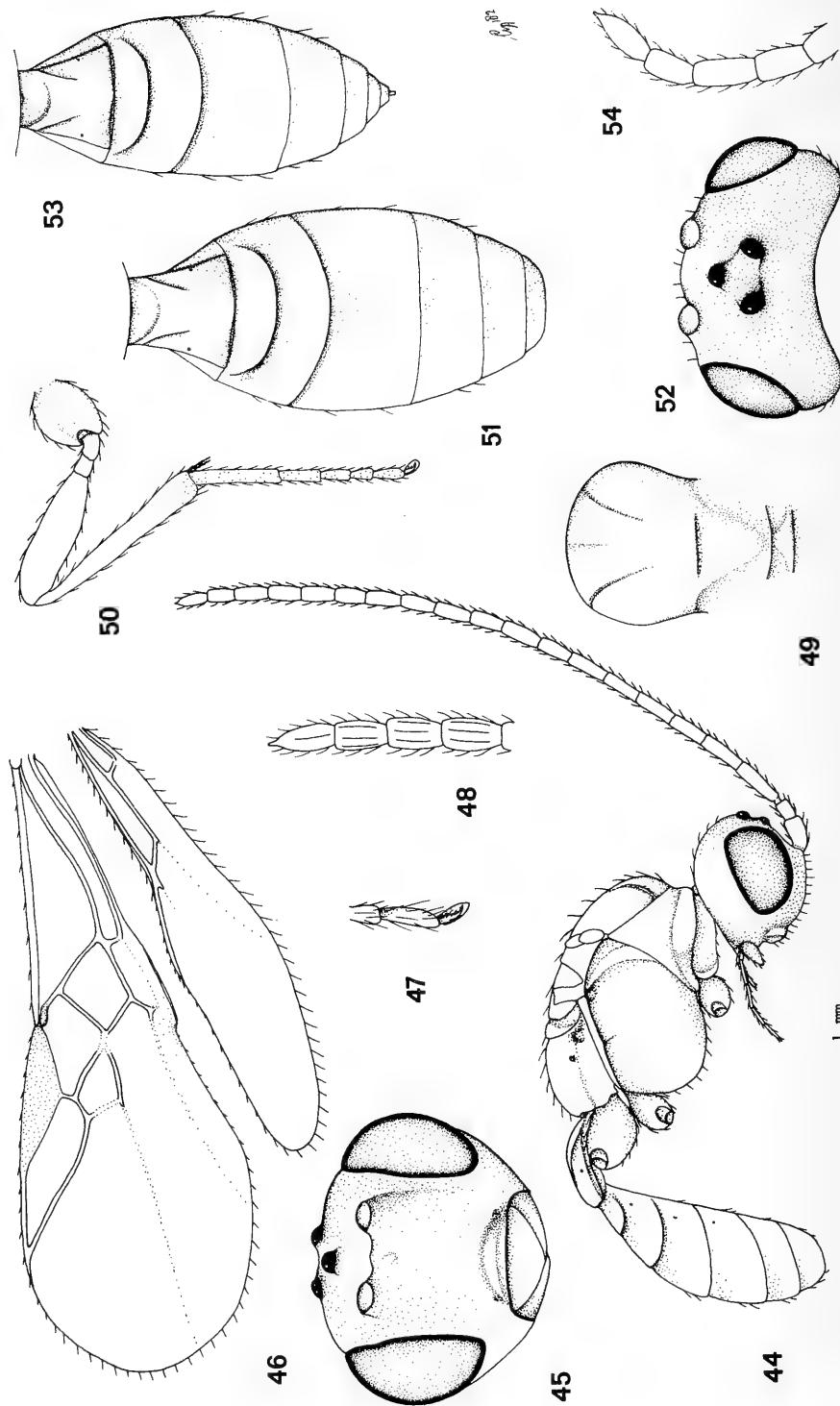
Figs. 10-19. *Gnaptodon apheres* spec. nov., holotype, ♀. 10. habitus, lateral aspect; 11, apex of antenna; 12, hind claw; 13, wings; 14, head, frontal aspect; 15, head, dorsal aspect; 16, palpi; 17, hind leg; 18, thorax, dorsal aspect; 19, 1st and 2nd tergites, dorsal aspect. Fig. 20. *Gnaptodon decoris* (Förster), Netherlands, Wijster, ♀, wings. Fig. 21. *Gnaptodon pilosus* spec. nov., paratype, ♂, wings (somewhat artificially bent). 10, 13, 17, 20, 21: scale-line, 1 ×; 11, 12, 14-16, 18, 19: 1.5 ×.



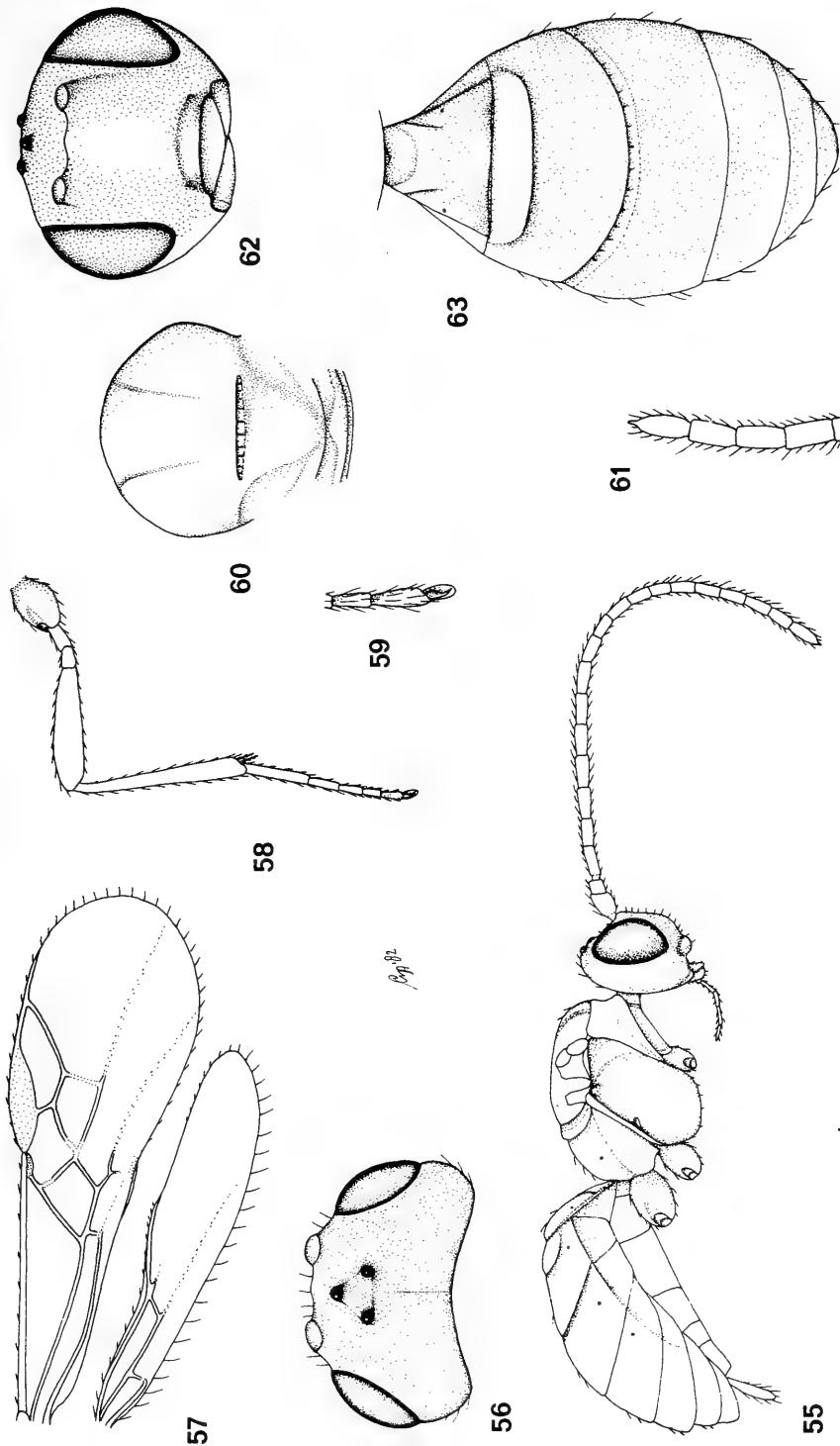
Figs. 22—33. *Gnaptodon pumilio* (Nees), neotype, ♀. 22, habitus, lateral aspect; 23, apex of antenna; 24, wings; 25, 1st subdiscal cell of fore wing; 26, thorax, dorsal aspect; 27, head, dorsal aspect; 28, fore wing apex; 29, hind leg; 30, hind leg; 31, 1st—3rd tergites, dorsal aspect; 32, head, frontal aspect; 33, hind leg. 22, 24, 29: scale-line, 1 X; 23, 25, 28, 30, 33: 2.5 X; 26, 27, 31, 32: 1.6 X.



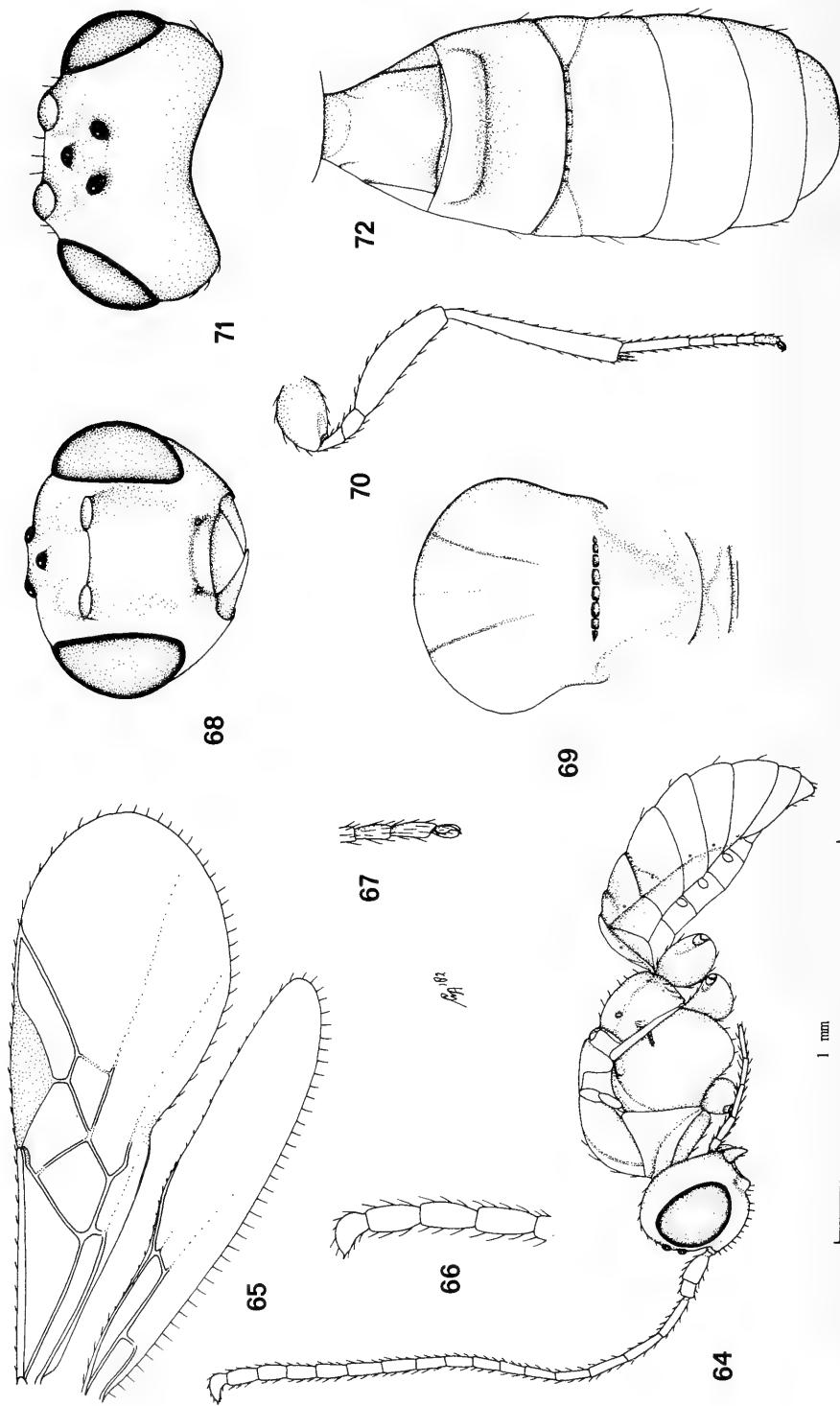
Figs. 34–43. *Gnaptodon orientalis* spec. nov., holotype, ♀. 34, habitus, lateral aspect; 35, antenna, lateral aspect; 36, hind claw; 37, wings; 38, head, frontal aspect; 39, head, dorsal aspect; 40, hind leg; 41, apex of antenna; 42, thorax, dorsal aspect; 43, 1st—3rd tergites, dorsal aspect. 34, 35, 37, 40: scale-line, 1  $\times$ ; 36, 41: 2.5  $\times$ ; 38, 39, 42, 43: 1.5  $\times$ .



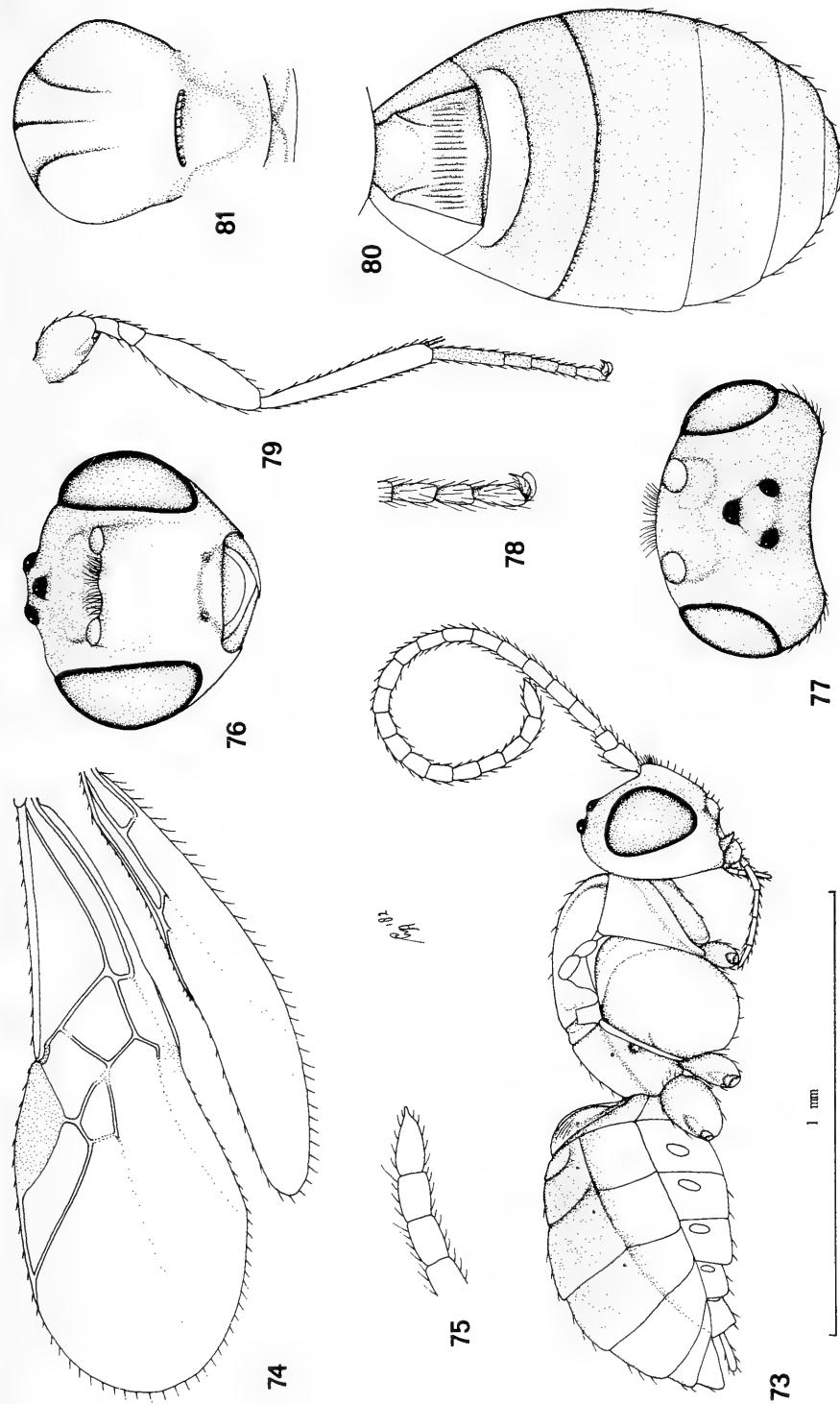
Figs. 44-54. *Gnapiodon georginae* spec. nov., holotype, ♂ (but 53 and 54 of ♀ paratype ex *Sigamella malella* (Strainton)). 44, habitus, lateral aspect; 45, head, frontal aspect; 46, wings; 47, hind claw; 48 and 54, apex of antenna; 49, thorax, dorsal aspect; 50, hind leg; 51 and 53, metasoma, dorsal aspect; 52, head, dorsal aspect. 44, 46, 50: scale-line, 1 × ; 45, 52: 1 × ; 47, 48, 54: 2 × ; 49, 51, 53: 1.2 × .



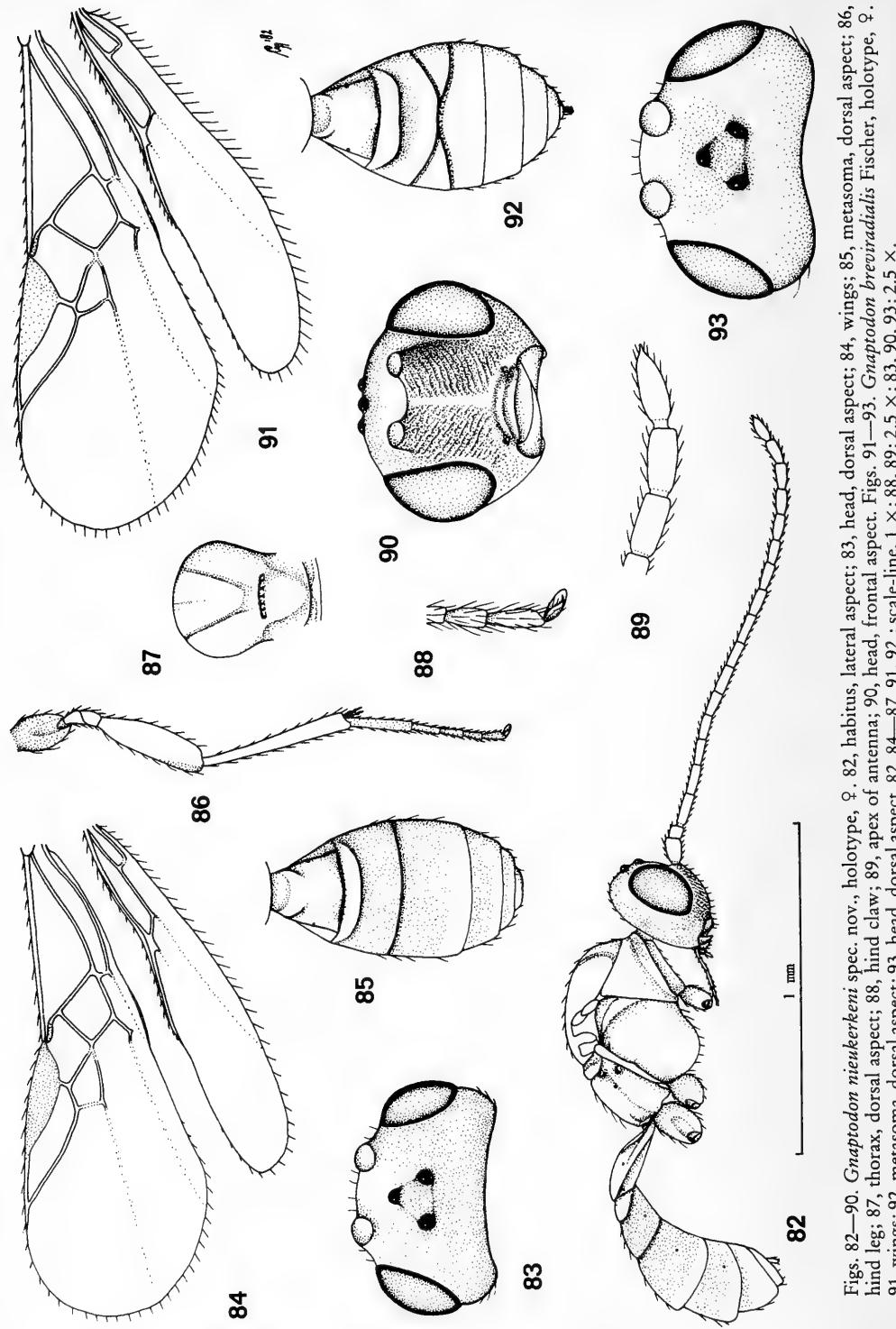
Figs. 55—63. *Gnaptodon brevis* spec. nov., holotype, ♀. 55, head, lateral aspect; 56, head, dorsal aspect; 57, wings; 58, hind leg; 59, hind claw; 60, thorax, dorsal aspect; 61, apex of antenna; 62, head, front aspect; 63, metasoma, dorsal aspect. 55, 57, 58: scale-line, 1 ×; 56, 60, 62, 63: 1.5 ×; 59, 61: 2 ×.



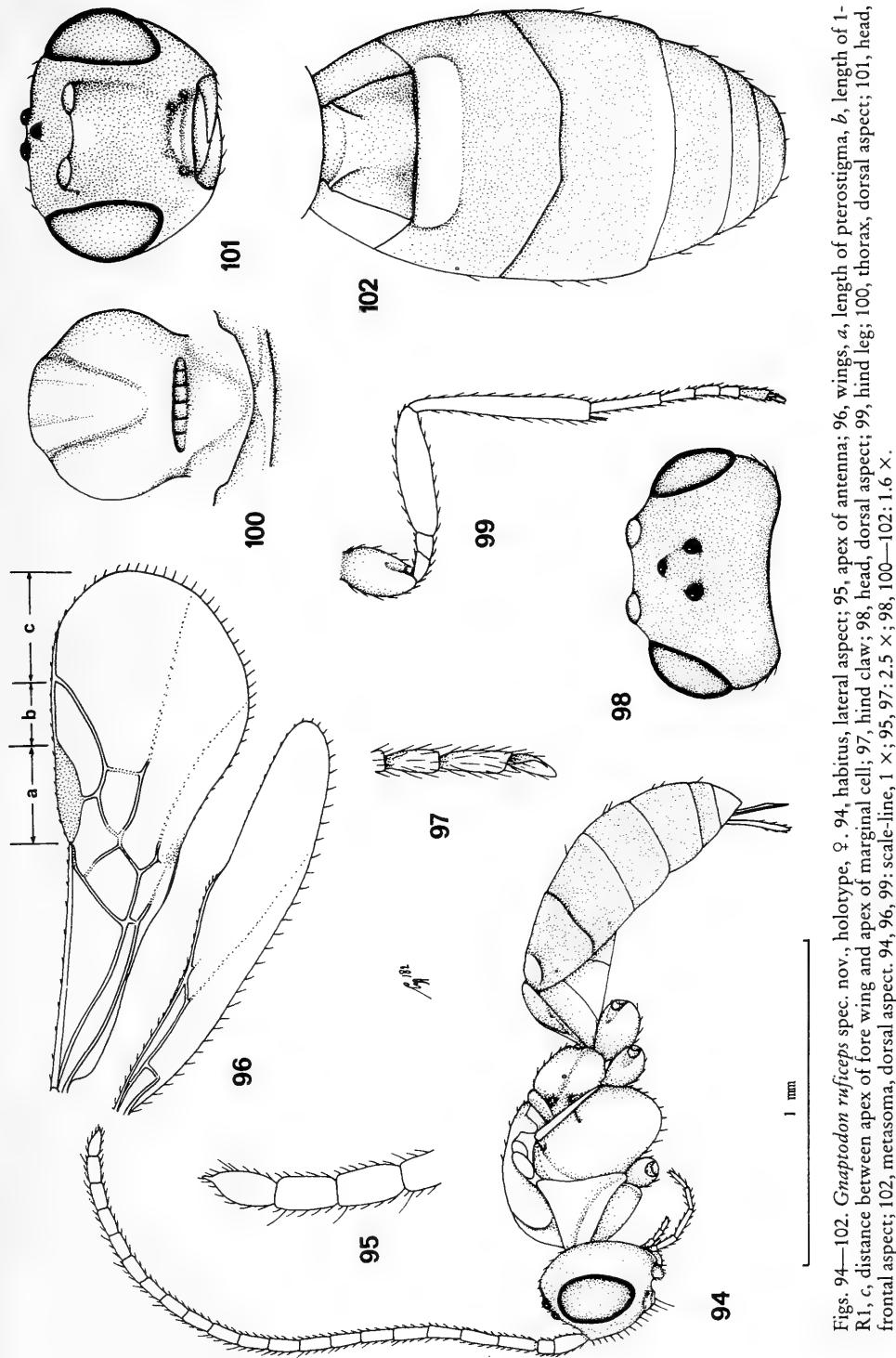
Figs. 64—72. *Gnaphotodon vlugi* spec. nov., holotype, ♂. 64, habitus, lateral aspect; 65, wings; 66, apex of antenna; 67, hind claw; 68, head, frontal aspect; 69, thorax, dorsal aspect; 70, head, dorsal aspect; 71, head, dorsal aspect; 72, metasoma, dorsal aspect. 64, 65, 70: scale-line, 1 mm. 66—69, 71, 72: 2 ×.



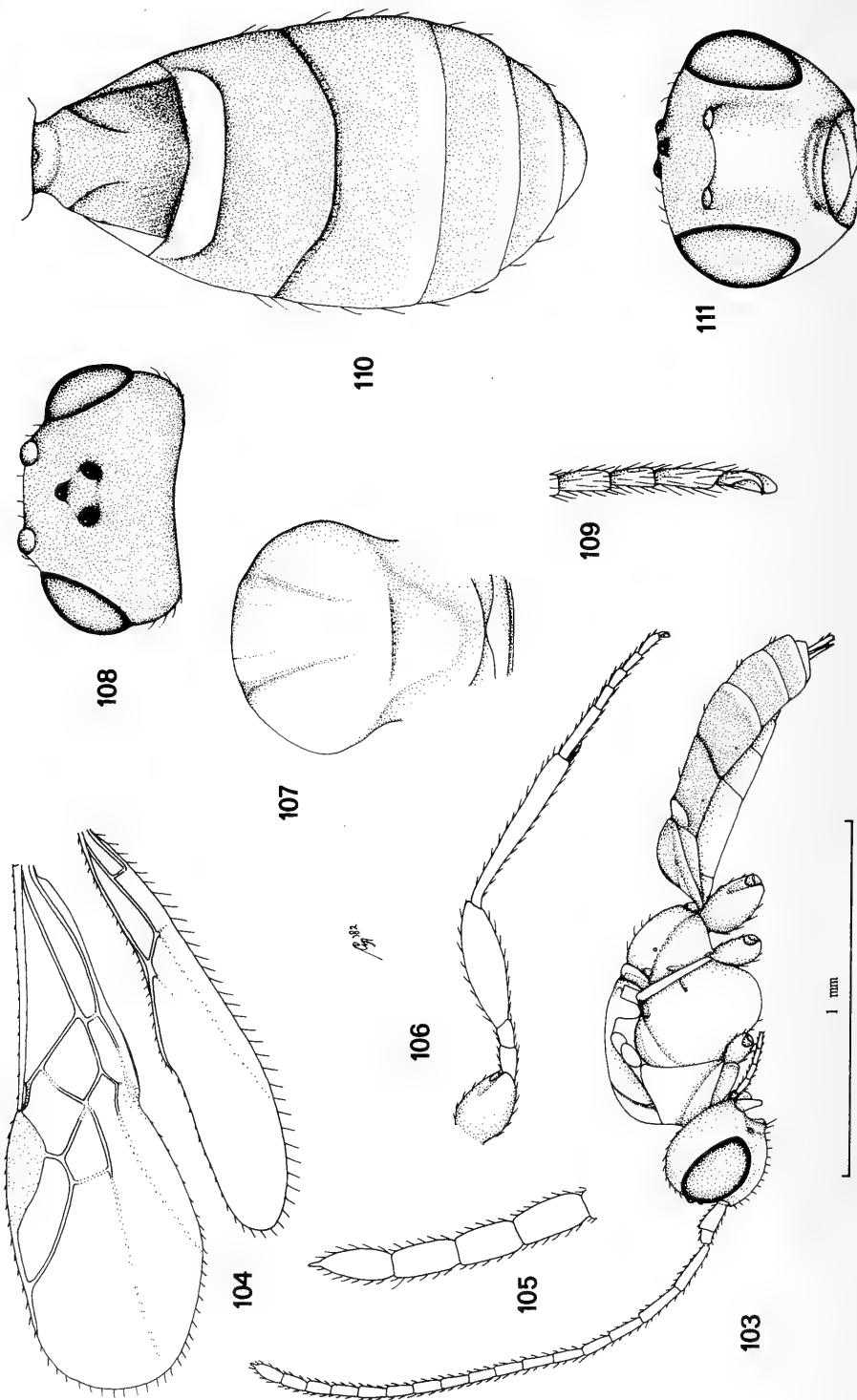
Figs. 73—81. *Gnaptodon pilosus* spec. nov., holotype, ♀. 73, habitus, lateral aspect; 74, wings; 75, apex of antenna; 76, head, frontal aspect; 77, head, dorsal aspect; 78, hind claw; 79, hind leg; 80, metasoma, dorsal aspect. 73, 74, 79: thorax, dorsal aspect; 75, 78: 1 ×; 76, 77, 80, 81: 1.5 ×.



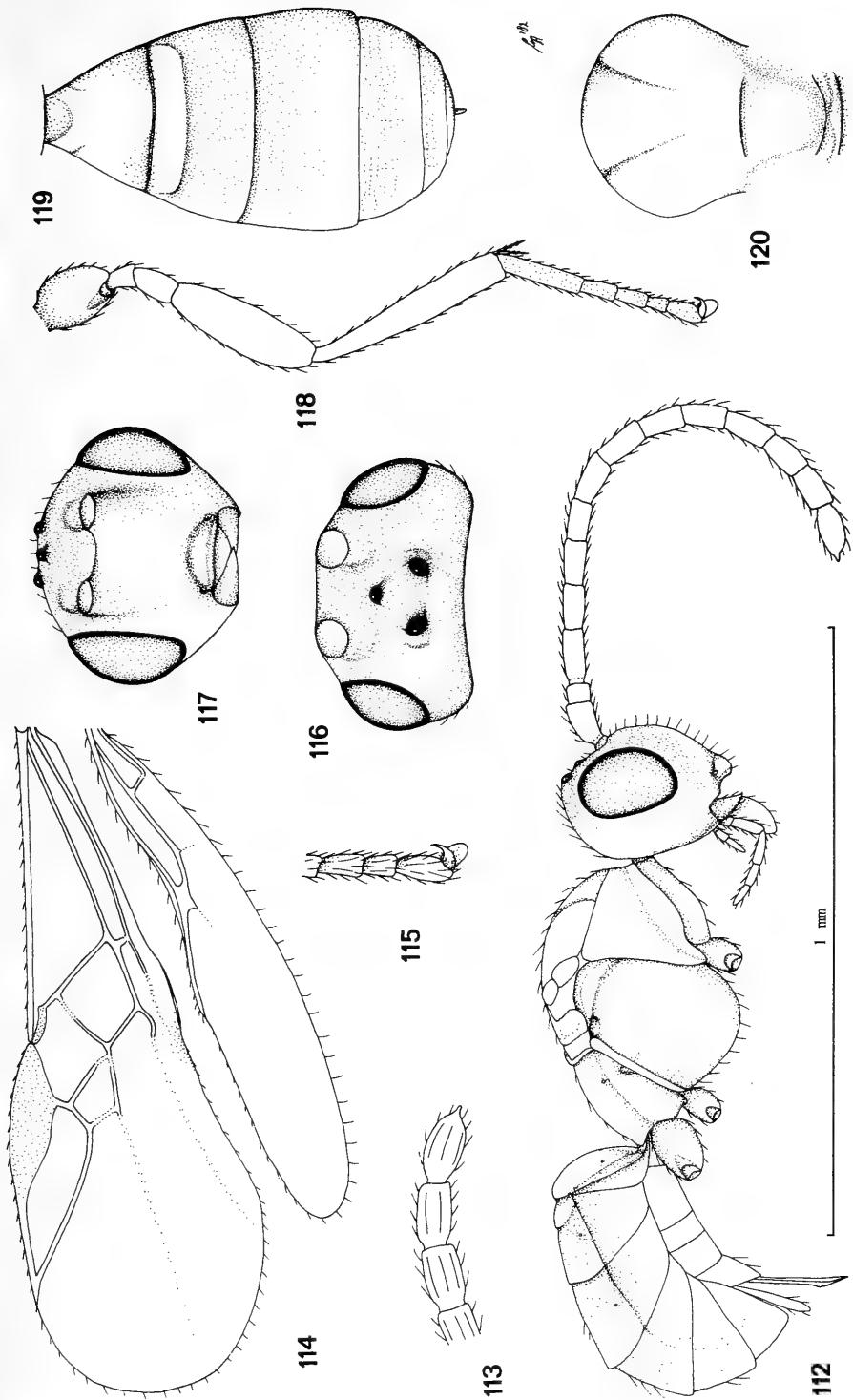
Figs. 82—90. *Gnaptodon nieukerkeni* spec. nov., holotype, ♀. 82, habitus, lateral aspect; 83, head, dorsal aspect; 84, wings; 85, metasoma, dorsal aspect; 86, hind leg; 87, thorax, dorsal aspect; 88, hind claw; 89, apex of antenna; 90, head, frontal aspect. Figs. 91—93. *Gnaptodon breviradiellus* Fischer, holotype, ♀. 91, wings; 92, head, dorsal aspect; 93, head, dorsal aspect. 82, 84—87, 91, 92 : scale-line, 1 ×; 88, 89: 2.5 ×; 83, 90, 93: 2.5 ×.



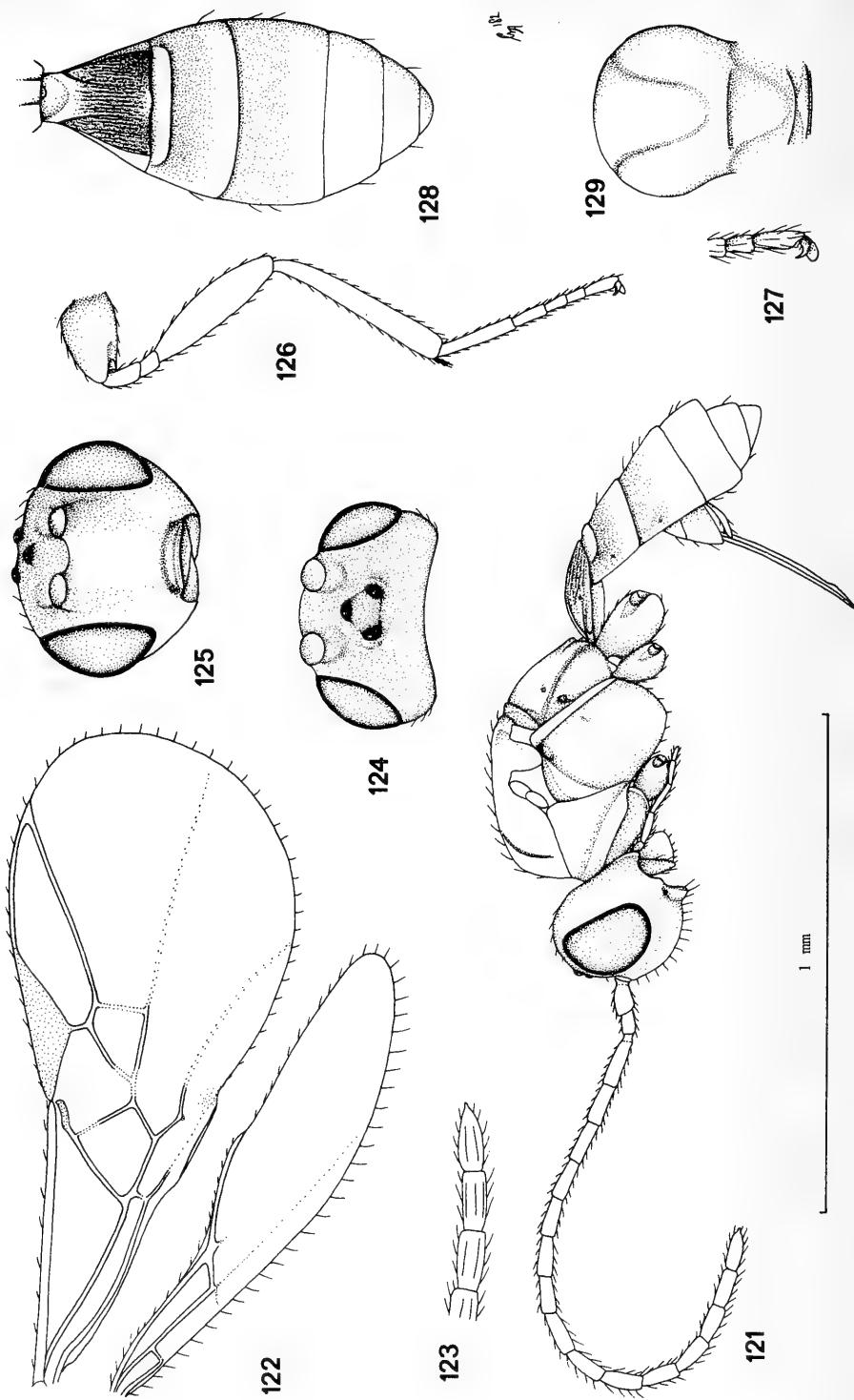
Figs. 94—102. *Gnaptodon ruficeps* spec. nov., holotype, ♀. 94, habitus, lateral aspect; 95, apex of antenna; 96, wings, *a*, length of prorostigma, *b*, length of 1-R<sub>1</sub>, *c*, distance between apex of fore wing and apex of marginal cell; 97, hind claw; 98, head, dorsal aspect; 99, head, frontal aspect; 100, hind leg; 101, head, frontal aspect; 102, metasoma, dorsal aspect. 94, 96, 99: scale-line, 1 ×; 95, 97: 2.5 ×; 98, 100—102: 1.6 ×.



Figs. 103—111. *Gnatptodon erasmi* spec. nov., holotype, ♀. 103, habitus, lateral aspect; 104, wings; 105, apex of antenna; 106, hind leg; 107, thorax, dorsal aspect; 108, head, dorsal aspect; 109, hind claw; 110, metasoma; 111, head, frontal aspect; 103, 104, 106, scale-line, 1 ×; 105, 109: 2.5 ×; 107, 108, 110, 111: 1.6 ×.



Figs. 112—120. *Gnaptodon bini* spec. nov., holotype, ♀. 112, habitus, lateral aspect; 113, head, frontal aspect; 114, wings; 115, hind claw; 116, head, dorsal aspect; 117, head, lateral aspect; 118, hind leg; 119, metasoma, dorsal aspect; 120, head, lateral aspect. 112, 114, 118, dorsal aspect; 113, 115, 116, 117, 119, 120: 1.3 ×.



Figs. 121—129. *Gnaptodon similis* spec. nov., holotype, ♀. 121, habitus, lateral aspect; 122, wing; 123, apex of antenna; 124, head, dorsal aspect; 125, head, frontal aspect; 126, hind leg; 127, hind claw; 128, metasoma, dorsal aspect; 129, thorax, dorsal aspect. 121, 122, 126, scale-line, 1 ×; 123, 127: 1.6 ×; 124, 125, 128, 129: 1.2 ×.

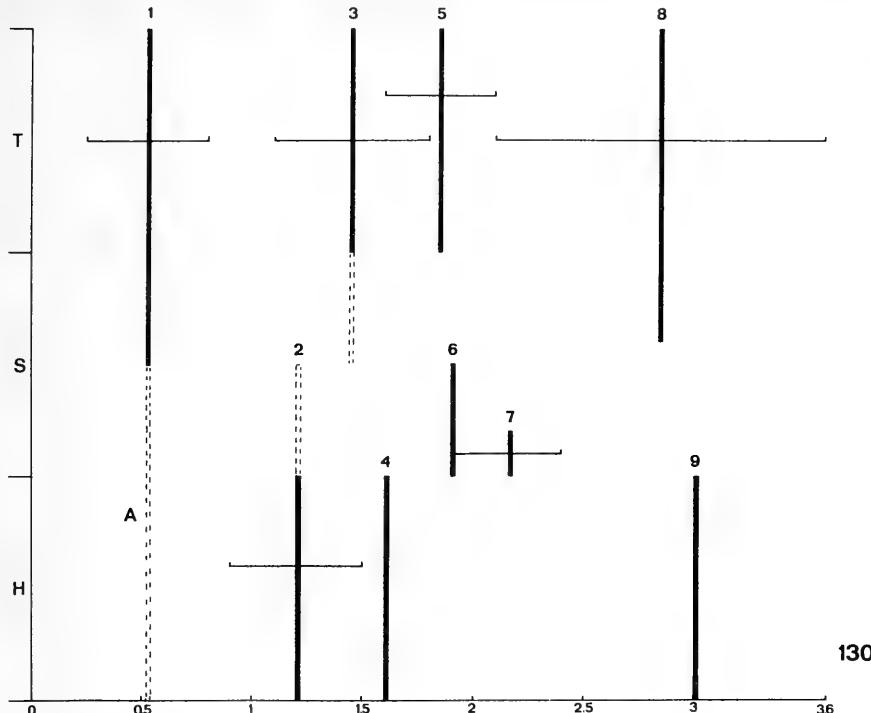


Fig. 130. Diagram depicting the vegetation zone wherein the host occur versus the indices of distance between the apex of the fore wing and the apex of the marginal cell ("c" in fig. 96) and length of vein 1-R1 ("b" in fig. 96). 1, *Gnaptodon pumilio* (Nees); A, form A; 2, *G. decoris* (Foerster); 3, *G. georginae* spec. nov. (in trees except *Quercus*); 4, *G. ruficeps* spec. nov.; 5, *G. pilosus* spec. nov. (in *Quercus*); 6, *G. erasmi* spec. nov.; 7, *G. nieukerkeni* spec. nov.; 8, *G. breviradialis* Fischer; 9, *G. brevis* spec. nov.; T, tree zone; S, shrub zone; H, herb zone.

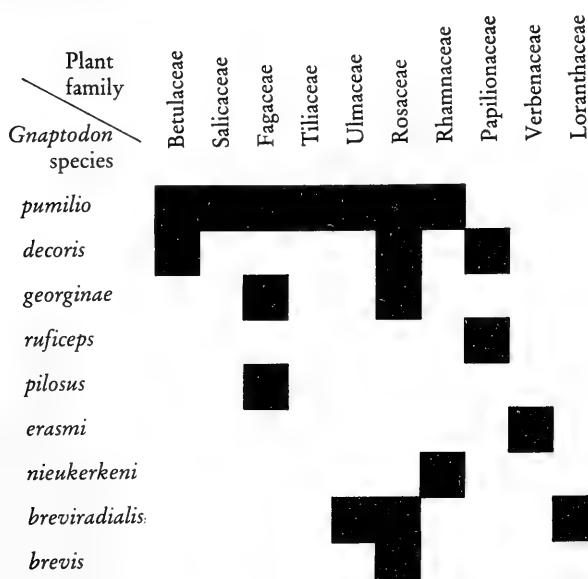


Fig. 131. The occurrence of *Gnaptodon* species in plant families infested by Nepticulidae.







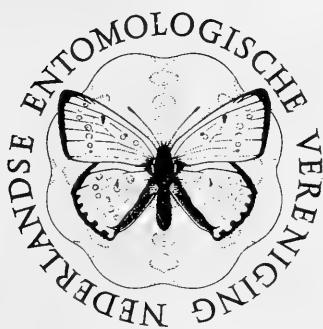




# TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING



## INHOUD

TH. C. M. BROCK and G. VAN DER VELDE. — An autecological study on *Hydromyza livens* (Fabricius) (Diptera, Scatomyzidae), a fly associated with nymphaeid vegetation dominated by *Nuphar*, pp. 59—90, figs. 1—25.



# AN AUTECOLOGICAL STUDY ON *HYDROMYZA LIVENS* (FABRICIUS) (DIPTERA, SCATOMYZIDAE), A FLY ASSOCIATED WITH NYMPHAEID VEGETATION DOMINATED BY *NUPHAR*<sup>1)</sup>

by

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## ABSTRACT

The life history and autecology of the fly *Hydromyza livens* (Fabricius) were investigated in detail in two Dutch waters. Special attention was paid to its effects on and interrelations with vegetation dominated by *Nuphar lutea* (L.) Sm. The food plants, geographical distribution, aspects of population dynamics and the morphology of *H. livens* are described and discussed.

Investigations have been made on general behaviour, feeding behaviour, spatial occurrence, sexual behaviour, sex ratio, oviposition, mortality and predation of the adults. The function of the chorion of the egg is discussed. Some experiments have been carried out to study the development of the eggs in relation with humidity, oxygen and temperature. The process of hatching, feeding behaviour, mine patterns, the effect of temperature on feeding behaviour and the mortality of the larvae are described. Data are given of the position in the leaf stalks, emergence and hibernation of the pupae.

The life history of *H. livens* is compared with that of *H. confluens* Loew, a species bound to *Nuphar* in North America.

## INTRODUCTION

Nymphaeid vegetations, which are very common and show an optimal development in The Netherlands, have been studied by us during several years. Nymphaeids are aquatic plants with floating leaves, which root in the bottom and have flowers above or floating on the water surface. Because of their structure they have an important function as a habitat for semi-aquatic insects.

The species *Hydromyza livens* (Fabricius, 1794) (syn. *Musca livens* Fabricius, 1794, and *Nupharia rivularis* Robineau-Desvoidy, 1830) of the dipteran family Scatomyzidae (syn. Cordyluridae, Scatophagidae) is such an insect occurring abundantly on the nymphaeids studied, especially on *Nuphar lutea* (L.) Sm. The larvae of most species belonging to this family live in dung; only a few genera are known to mine in leaves or petioles of plants (Sack, 1937). According to Hering (1926) the larvae of most *Hydromyza* species mine the leaves and/or petioles of Liliaceae and Orchidaceae.

*Hydromyza livens*, however, can complete its whole life cycle on *Nuphar lutea* (Nymphaeaceae), one of the nymphaeid species of which the structure and function is a subject of investigations in our laboratory. The larvae of *H. livens* mine the floating leaves of *Nuphar*. By their consumption of living plant tissue, the larvae are an important link in the grazer food chain and decomposition processes connected with *Nuphar lutea*. Because of our interest in these interrelations the life history and habits of *H. livens* were studied in detail and a review was made of the literature.

Furthermore the results of our study could be compared with those of Welch (1914, 1917) who studied the North American species *H. confluens* Loew, 1863, of which the life history and habits resemble those of *H. livens* in many ways.

## DESCRIPTION OF THE STUDY AREAS

Most observations have been made in the Oude Waal near Nijmegen (municipality of Ubbergen, Province of Gelderland); some additional observations have been made in the Haarsteegse Wiel (municipality of Vlijmen,

<sup>1)</sup> Contribution no. 19 of the Nymphaeid Project.

Province of Noord-Brabant). In both water bodies pure stands of *Nuphar lutea* occur. The waters differ, however, in their dimensions, water quality and bottom composition.

The Oude Waal (fig. 1) is an old river branch cut off from the river Waal, where extensive nymphaeid vegetation dominated by *Nuphar lutea*, *Nymphaea alba* L. and *Nymphaoides peltata* (Gmel.) O. Kuntze occur. It consists of a large shallow water body, 1 km in length and about 250 m wide, and three interconnected ponds (fig. 1, D, E and F). The depth of the large shallow water body varies from 0.5 to 1.5 m; in the dry summer of 1976 it became almost completely dry. About once every two years the area is flooded in winter or spring by water from the river Waal; summer high waters occur only occasionally. The depth of the three interconnected ponds increases towards their centres to 2.5, 5.5 and 5.5 m, respectively (D, E and F). The bottom of the Oude Waal consists of a pattern of clay and sand, sometimes mixed, covered by a sapropelium layer of varying thickness.

The Haarsteegse Wiel (fig. 1) originated from two, but not simultaneous, bursts in the dike of the river Meuse. This water body has a surface area of 17.9 ha (44.2 acres) and a maximum

depth of 17 m. The nymphaeid vegetation dominated by *Nuphar lutea* and *Nymphaea candida* Presl, is almost completely restricted to the southern and western parts of the lake, where they are sheltered against wave- and wind action. The bottom of the Haarsteegse Wiel consists mainly of sand (wash-over deposits), but where nymphaeids grow there is a layer of sapropelium, becoming thicker towards the littoral border. The hydrology of the lake is dependent on rain and ground water only; the water-level shows only small fluctuations.

Apart from the two described areas of investigation several waters in The Netherlands with vegetation dominated by *Nuphar* have been visited and checked for floating leaves with mines of the larvae of *H. livens*.

#### GEOGRAPHICAL DISTRIBUTION AND FOOD PLANTS

The ecological distribution of *H. livens* is mainly governed by its affinity for the food plants on which the larvae feed and on which they can complete their life-cycle.

In table 1 a literature review is given of the food plants of the larvae of *H. livens*. According to most authors the larvae mine in the leaves

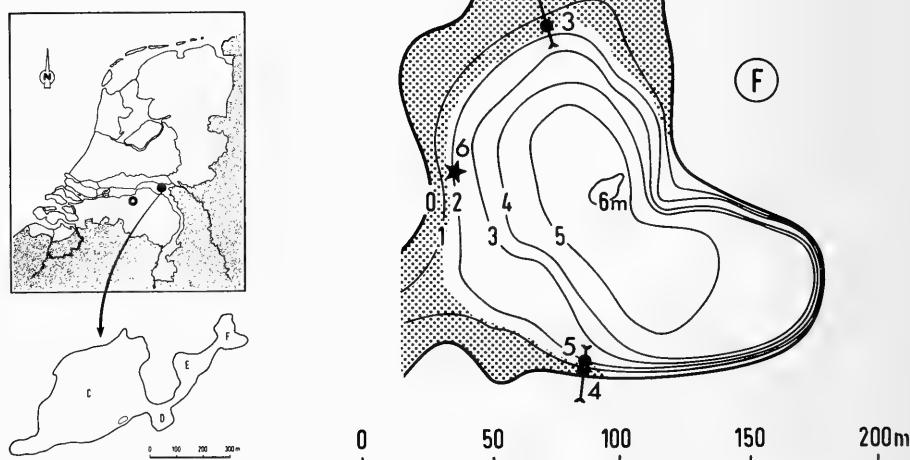


Fig. 1. Left side: the location of the areas studied in The Netherlands (open dot: Haarsteegse Wiel, closed dot: Oude Waal). Right side: bathymetric map of pond F of the Oude Waal, showing the nymphaeid beds (dotted area), the situation of transects studied in the *Nuphar* zone and the isolated *Nymphaea* bed (indicated by an asterisk).

Table 1. Review of the food plants of *H. livens* as mentioned in the literature.

Taxon	Author
Nymphaeaceae	Collin, 1958
<i>Nymphaea</i>	Wesenberg-Lund, 1943
<i>Nymphaea alba</i> L.	De Meyere, 1940
<i>Nuphar</i>	Hackman, 1956; Vockeroth, 1978
<i>Nuphar lutea</i> (L.) Sm.	De Meyere, 1895; Eberle, 1943; Gercke, 1877; Brauer, 1883; Hendel, 1928; Gaevskaya, 1966; Grünberg, 1910; Hering, 1926; Heslop-Harrison, 1955; Monchadskii, 1940; Sack, 1937; Seguy, 1934; Schütte, 1921; Van der Velde, 1978; Van der Velde et al., 1978
<i>Nuphar pumila</i> (Timm) DC.	Heslop-Harrison, 1955
<i>Nuphar × intermedia</i> Ledeb.	Heslop-Harrison, 1955
<i>Caltha palustris</i> L.	Gaevskaya, 1966; Monchadskii, 1940

and petioles of *Nuphar lutea*. This is confirmed in the present study; in all investigated Dutch waters with *Nuphar* stands floating leaves with mines of *H. livens* larvae were found. Heslop-Harrison (1955) mentioned *H. livens* larvae also from the leaves and petioles of *Nuphar pumila* (Timm) DC. and *Nuphar × intermedia* Ledeb. (= *N. lutea* × *N. pumila*). They were also found by us in floating leaves of *N. × intermedia*. It can be concluded from these data that all European *Nuphar* species are adequate food plants for *H. livens*. In the botanical garden of Haren (State University of Groningen, The Netherlands) the second author of this paper observed floating leaves of the North-American *Nuphar advena* Ait. with mines of *H. livens*. The occurrence of *H. livens* in America has not been reported.

In the literature there is some misunderstanding concerning the plant species on which *H. livens* can complete its life-cycle. De Meijere (1940) reported the occurrence of *H. livens* larvae in floating leaves of *Nymphaea alba*; in his paper, however, a drawing of a *Nuphar* leaf with mines of *H. livens* is given. In Wesenberg-Lund's "Biologie der Süßwasserinsecten" (1943) an obscure picture of *Hydromyza* mines in a so-called *Nymphaea* leaf is shown. Eberle (1943), however, who transplanted *Hydromyza* larvae from *Nuphar* leaves to *Nymphaea* leaves, and also to other *Nuphar* leaves, concluded that the transplanted larvae fail to develop in floating leaves of *Nymphaea*. We confirmed this in the laboratory for transplanted larvae in leaves of *Nymphaea alba* and *Nymphaea candida*. We never observed *Hydromyza* larvae in *Nymphaea* leaves.

According to Gaevskaya (1966), Monchadskii (1940) reported the occurrence of *Hydromyza* mines in leaves of *Caltha palustris* L.; this fact, however, is neither confirmed by other literature sources nor observed by the authors of the present paper.

Therefore, it can be concluded that in Europe *H. livens* is strictly bound to *Nuphar* species.

In the Limnofauna Europaea, Vockeroth (1978) reported several distribution areas for *H. livens* (see fig. 2), viz.:

(A) Areas with real records: the western secondary mountain chain (8), the central secondary mountain chain (9), the western lowlands (13), the central lowlands (14), Ireland (17) (Coon River near Partry, North of Lough Mask, 3 July 1982 on *Nuphar lutea* (L.) Sm. (G. van der Velde), the United Kingdom (18), Northern Sweden (22), Taiga (23), Uzbekistan, Siberia;

(B) Areas in which *H. livens* is expected to occur: the Alps (4), the Carpathians (10), the Hungarian lowlands (11), the Baltic Province (15), the eastern lowlands (16);

(C) An area in which *H. livens* does absolutely not occur: Iceland (19).

The distribution of *H. livens* does not extend beyond the confined distribution of the genus *Nuphar* in Europe. In fig. 2 both the geographical distribution of *Nuphar* (according to Meusel et al., 1965) and *H. livens* (according to Vockeroth, 1978) are compared. Both distribution areas coincide nearly perfectly. When considering fig. 2, the statement in the Limnofauna Europaea that *H. livens* does not occur in Iceland (19) is quite obvious, because *Nuphar* does not occur there either. On account of the geo-



Fig. 2. Map of the European distribution of both the genus *Nuphar* (dotted areas) (modified after Meusel et al., 1965) and *H. livens* (areas with numbers according to Limnofauna Europaea).

graphical distribution of *Nuphar*, *H. livens* might also be expected to occur in other regions such as Italy, the Balkans and Norway.

#### DEVELOPMENT IN TIME

In order to obtain an idea of the population dynamics of *H. livens* the occurrence in time of adults and larvae was quantified in various ways. Both the larval and adult stage can be easily recognized in the field. Adult *H. livens* can be found on the upper side of the nymphaeid floating leaves; the flies are not adapted to walking over the water surface, they have to fly from leaf to leaf. To quantify adult *H. livens* in time the insect-lime method was used (adhesive or sticky trap).

The mine tracks of the larvae of *H. livens* in the floating *Nuphar* leaves can be easily recognized and counted. To quantify the larvae and the number of affected floating leaves in time, the leaf-marking method was used.

The quantitative data of adults and larvae are

dealt with together in order to maintain an overall picture of the various generations of *H. livens* per year.

The insect-lime method. — Each week, from June until October, 1977, six undamaged floating leaves (five of *Nuphar lutea* and one of



Fig. 3. Adhesive trap (for explanation, see text).

*Nymphaea alba*) of the same size were gathered in the Oude Waal, pond F, and covered with insect-lime (Tangletrap or Stikem), which has no odour and consequently does not attract or repel the insects. These leaves, of which the petioles were removed, were attached onto six other floating leaves and then protected from predation by birds by wire netting (with meshes of 3 cm) which was supported by cork floaters (fig. 3). The wire netting with cork floaters was attached with a string to the petiole of the supporting leaf. After 24 hours these leaves were taken to the laboratory in plastic bags, so that the catch remained as undamaged as possible. The fauna was washed from the floating leaves with refined petrol and then fixed in 70% alcohol.

The leaves were laid out in transects from the littoral border vegetation to the open water, so that the distribution of the animals over the entire nymphaeid zone could be studied (see section on spatial occurrence on the nymphaeids, further below).

**Leaf-marking method.** — During two years (1976 and 1977) floating leaves and flowers of *Nuphar lutea* have been marked with 12 mm Rotex-tape on which a number was printed with a Universal 12 printer. One end of the tape was fixed around the petiole by means of a staple and the other end was drawn through the leaf-sinus and then bent over the leaf surface like a flag so that it could be easily read (fig. 4).

One plant forms too many leaves to follow the development in detail so that plots of one square metre were made with frames of PVC tubes. The perforated tubing was sunk into the water and held at approximately 15 cm depth by using a string-corner attachment to cork float-

ers. Each frame was anchored (Van der Velde, 1980). Observations and marking of newly unrolled leaves took place every week during the season. The marking of floating leaves made it possible to study the numbers of mines and the numbers of affected leaves per plot per time. Temperatures of air and water were read regularly.

**Results.** — In fig. 5 the leaf-marking observations for 1976 in the Oude Waal are presented; the summer of that year was characterized by a longlasting drought resulting in the emergence of parts of the *Nuphar* vegetation.

The numbers of mines, the numbers of affected leaves, and their percentages of the total numbers of floating leaves per plot, show the same tendency (fig. 5). The number of mines and affected floating leaves of *Nuphar* per plot remained relatively low in the months of May, June and July, while at the end of August and in the beginning of September the numbers of larval *H. livens* clearly reached their maximum. Also the quantity of mines per floating leaf was at its maximum in this period (fig. 5).

Figs. 6 and 7 present the data of 1977 in the Oude Waal (marking-method and insect-lime method) and the Haarsteegse Wiel (marking-method). The summer of 1977 was quite normal without droughts. At the end of May and the beginning of June small numbers of *H. livens* larvae occurred in both waters. The quantity of affected leaves reached a maximum in the Haarsteegse Wiel from the last week of July until the second half of September. The larval population of *H. livens* in the Oude Waal was also large in this period with a small peak at the end of July and an absolute maximum in the last week of August.

The data concerning the adult stage of *H. livens*, obtained with the insect-lime method, are summarized in table 2 and fig. 6. Among the total catch of approximately 23,158 specimens (of which 99.4 Hexapoda and 0.6% Arachnida) 1,055 specimens were adult *H. livens*, i.e. 4.56% of the total catch (see for some other results Van der Velde (1978), Van der Velde & Brock (1980) and Van der Velde (1980)). The highest numbers of adult *H. livens* were caught from 18 August until 8 September.

**Discussion.** — With respect to the insect-lime method one should keep in mind that the result is not only dependent on the size of the *H. livens* population, but also on changes in the activity pattern of adult *H. livens* as, for example, caused by weather conditions. This is also valid

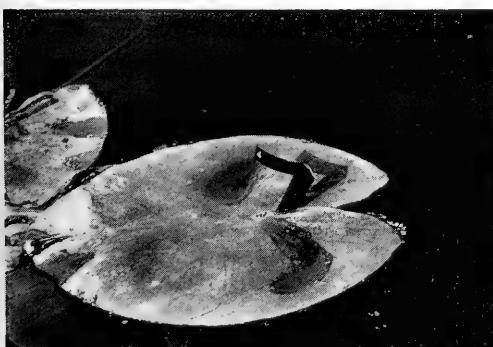


Fig. 4. A *Nuphar* leaf, marked with rotex tape (leaf-marking method).

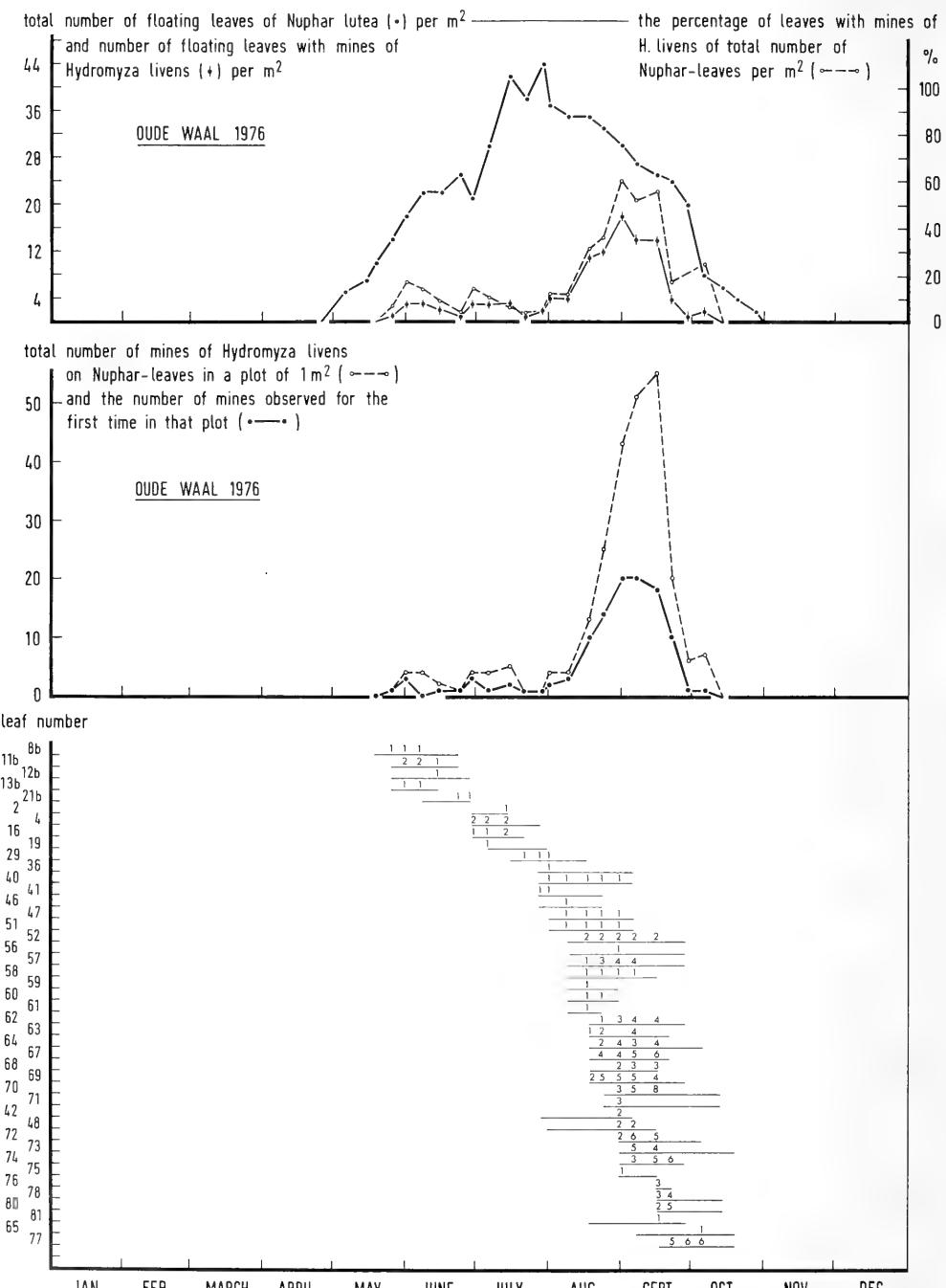


Fig. 5. Above: Total number of *Nuphar* leaves and absolute numbers and percentages of *Nuphar* leaves affected by *H. livens* per  $m^2$ , during 1976, in the Oude Waal. Middle: Total number of *Hydromyza* mines in a  $1m^2$  *Nuphar* plot and the number of mines observed for the first time in that plot, during 1976. Below: The presence in time of all *Nuphar* leaves which were affected by larvae of *H. livens* in a plot of  $1m^2$ . Each line represents the occurrence in time of an affected floating leaf. The numbers above these lines represent the numbers of mine tracks of *H. livens* in these leaves.

Table 2. Number of adult *H. livens* caught with insect-lime on floating leaves from 16 June until 29 September, 1977. For the localities of the different leaves see fig. 1 and the text.

Date 1977	Leaf number	Number of <i>H. livens</i> caught						Total number of insects and spiders caught	% <i>H. livens</i> of total catch
		1 Broad <i>Nuphar</i> zone	2	3	4 Narrow <i>Nuphar</i> zone	5	6 <i>N. alba</i>	Total	
16-VI	—	—	—	—	—	—	—	1401	—
23-VI	1	—	—	—	—	—	1	715	0.14
30-VI	1	—	2	—	3	1	7	1195	0.59
8-VII	3	7	12	3	7	2	34	2234	1.52
12-VII	7	7	2	6	7	—	29	3168	0.92
21-VII	7	12	4	9	14	2	48	2287	2.10
28-VII	8	7	4	6	—	1	26	1284	2.02
5-VIII	15	9	6	—	5	3	38	1580	2.41
12-VIII	7	17	20	—	7	10	61	1578	3.87
18-VIII	54	22	66	15	20	20	197	1322	14.90
25-VIII	33	88	64	29	14	13	241	1303	18.50
1-IX	12	13	54	2	33	12	126	1421	8.87
8-IX	16	68	66	14	21	5	190	1876	10.13
15-IX	7	11	15	3	3	5	44	762	5.77
22-IX	—	4	9	—	—	—	13	584	2.23
29-IX	—	—	—	—	—	—	—	448	—
Total number per leaf		171	265	324	87	134	74	1055	23158
									4.56

for the other insects, so that percentages of *H. livens* with respect to the total catch per date have been calculated (table 2). The absolute numbers and percentages showed the same trend, so that the catch gives a realistic picture of the adult population development in time.

When considering figs. 5, 6 and 7 it is clear that the development of the population of both adult and larval *H. livens* is correlated with the development of the floating leaves of *Nuphar lutea*. The first mine tracks on the floating leaves can be recognized early in the growing season of *Nuphar*, and at the end both the total numbers of floating leaves per plot and the numbers of *H. livens* diminish with the same tendency.

From the data obtained it can be concluded that *H. livens* has two or three generations per year in the studied waters. The third generation of the year before, which has hibernated in the pupal stage, occurs in May and June and the number of animals is small. The experiment with the insect-lime started too late to show this generation in the adult stage; adult flies, however, were caught by us with a hand-net in this period.

In the Oude Waal adults of *H. livens* were observed in 1975 from 5 June until 29 September, and in 1977 from 23 May until 22 September. The first generation in the Oude Waal in

1977 was present as larvae in May and the first week of June; adults of this generation were present at the end of June and in July. The maximum of adults was on 21 July. The second generation was present as larvae in the second half of July and the beginning of August. The maximum of adults was reached on 25 August. The third generation was present as larvae at the end of August and the first half of September. This generation hibernates as pupa and the adults of this generation were present in the next spring.

The data from the Oude Waal in 1976 do not indicate so clear the occurrence of three generations, that year, however, was characterized by a longlasting drought. This may have caused the establishment of only a minor second generation.

The population data from the Haarsteegse Wiel show two peaks (fig. 7), a minor one in the second half of May and the first weeks of June (first generation) and a large one in the second half of July, August, September and October. That the second peak is spread out over such a long period probably indicates that the second and third generation overlap, resulting in one broad peak only, as shown in fig. 7.

It can be concluded from the numbers of affected leaves per plot that in the Oude Waal in 1977 the second larval generation is ca. 6 times larger than the first generation while the third

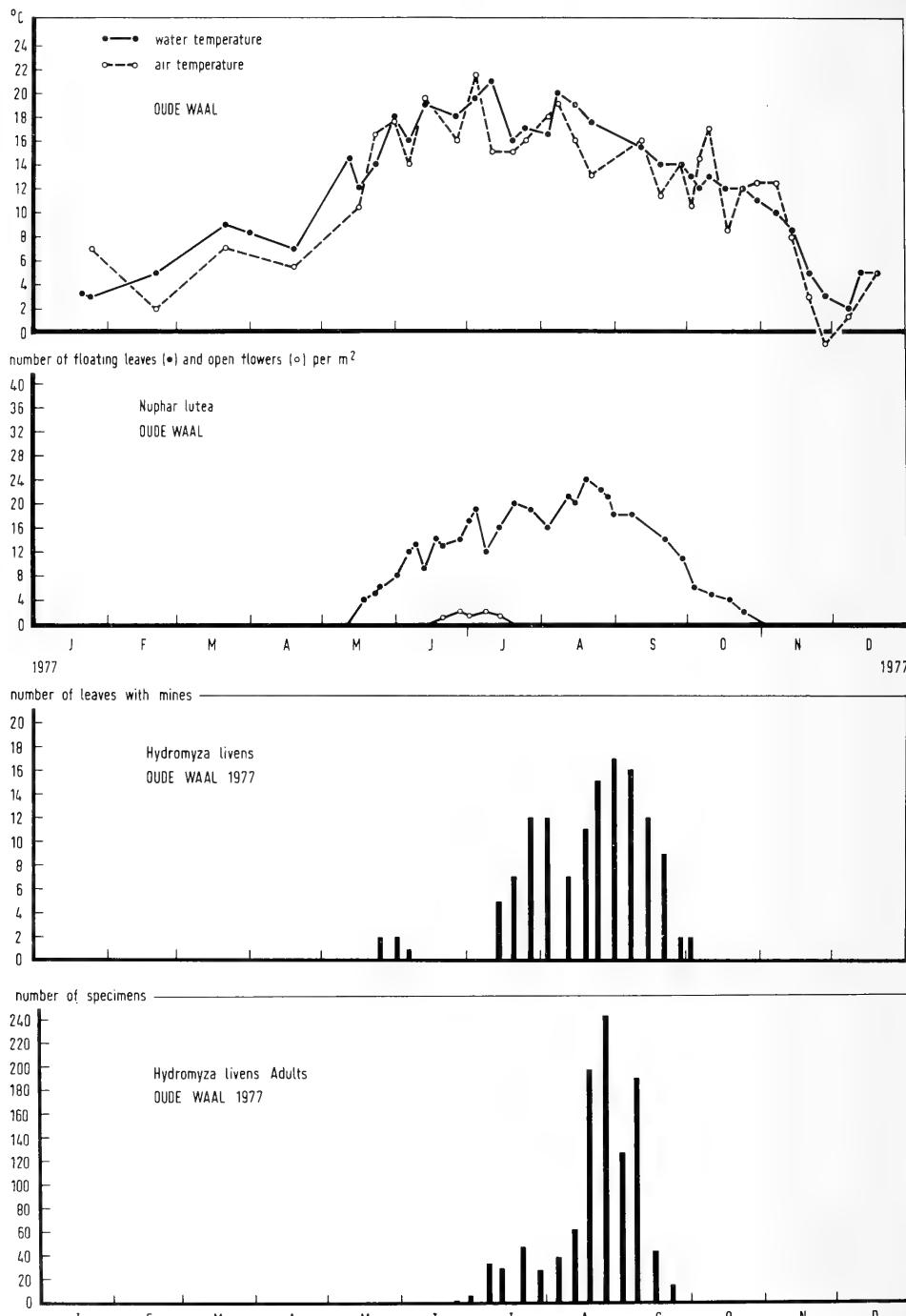


Fig. 6. Course of water and air temperature, presence of floating leaves and flowers of *Nuphar lutea* in a plot of 1 m<sup>2</sup>, numbers of floating leaves affected by *Hydromyza* larvae in that plot and numbers of adult *H. livens* caught with insect-lime on the floating leaves during 1977 on the Oude Waal.

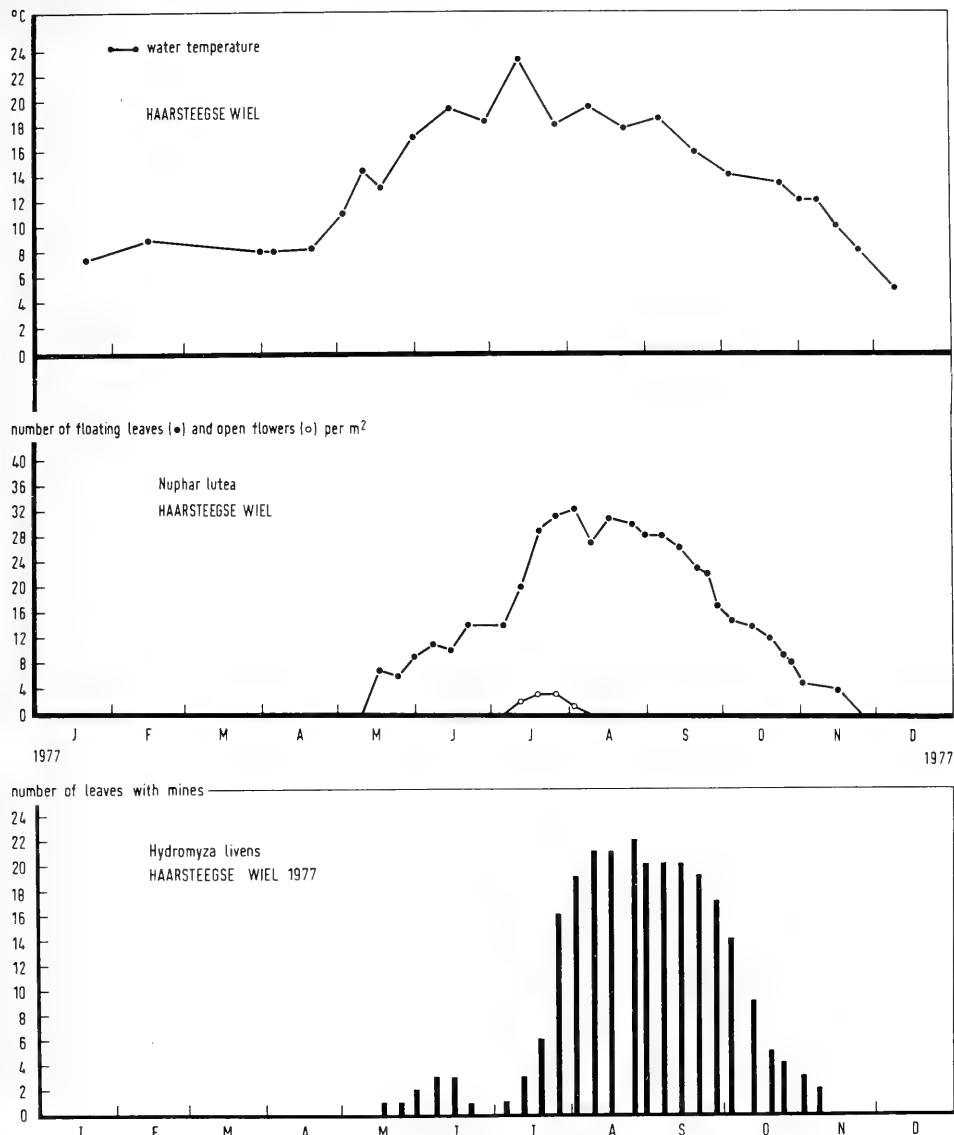


Fig. 7. Course of water temperature, presence of floating leaves and flowers of *Nuphar lutea* in a plot of 1 m<sup>2</sup> and numbers of floating leaves affected by *H. livens* in that plot during 1977 on the Haarsteegse Wiel.

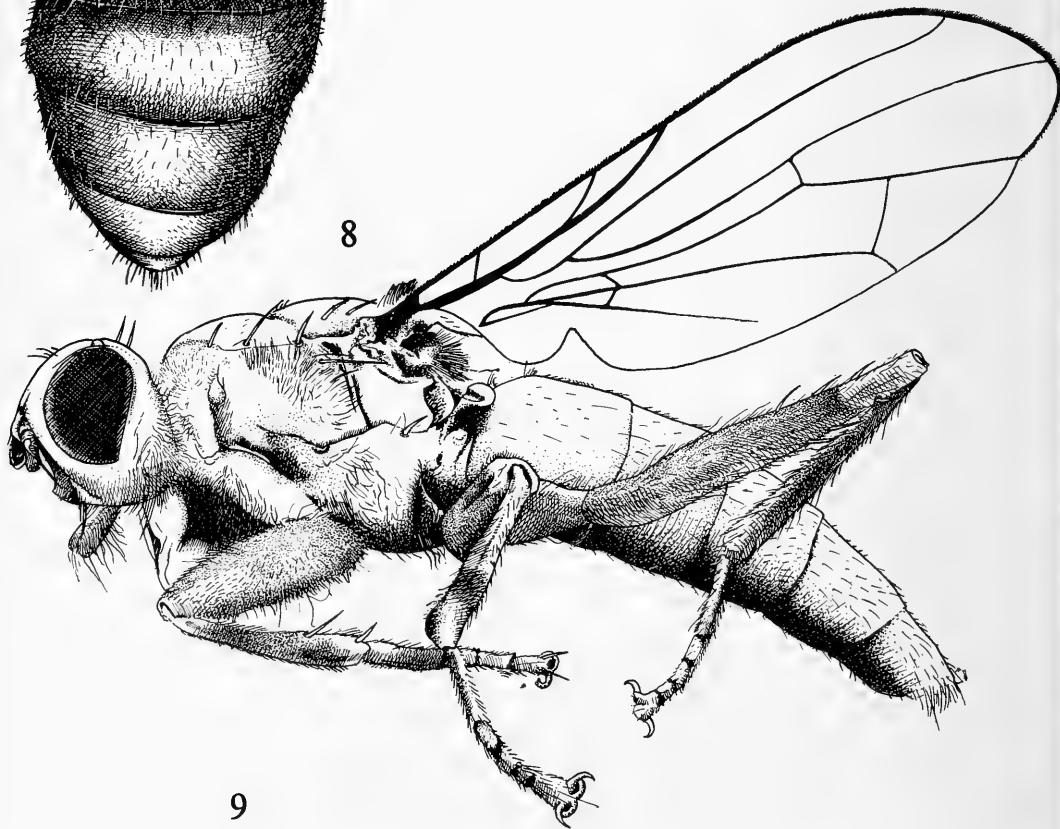
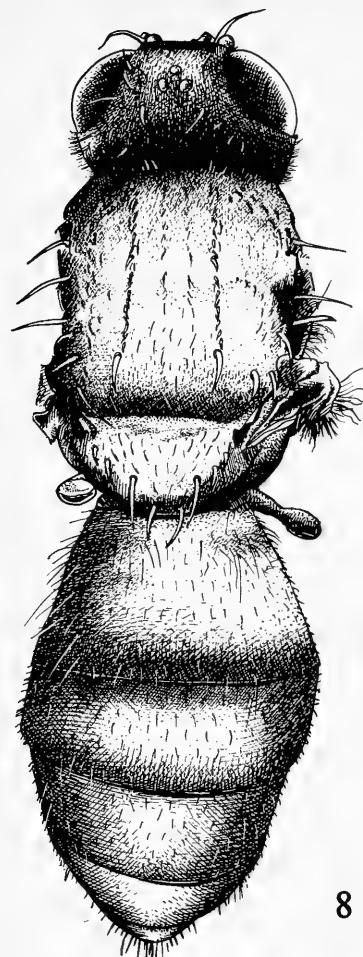
generation is ca. 8 times larger than the first one.

In the Haarsteegse Wiel in 1977 both the second and third larval generations are ca. 7 times larger than the first one.

The first, and under favourable conditions also the second, generation complete their life-cycle within the growing season of *Nuphar* while the pupae of the third (under bad environmental

circumstances probably also those of the second) generation hibernate and form the parents of the first generation, the next year.

That there are more generations per year is also supported by differences in behaviour and morphological characteristics of the larvae and pupae of the various generations, as will be discussed later. Schütte (1921) reported that summer and winter pupae are both present in the



beginning of August indicating that two generations overlap each other (see section on the pupa). The emergence of adults from summer pupae occurs in the same growing season of the food plant while the winter pupae hibernate. Schütte (1921) also suggested the possibility of the existence of three generations.

#### ADULTS

##### Morphological description

*H. livens* (fig. 8 and 9) is a fly of 7–9 mm length; the females (8–9 mm) are larger than the males (7–8 mm) (20 specimens of each sex were measured). The flies have a remarkably bright-yellow frons, chestnut-brown eyes and black antennae. The thorax and the abdomen are dusty blue-grey. The mesonotum has five more or less visible, grey-brown, longitudinal stripes. The legs are for the larger part red-

Fig. 8. Dorsal view of adult *H. livens* (wings omitted).

Fig. 9. Lateral view of adult *H. livens* (female).

brown, with yellow-brown ginglymae; the femora are partly blackish, tinged with a dusty blue-grey. The wings are of a translucent dusty-grey while the veins are slightly brownish. Veins R<sub>4+5</sub> and M are slightly convergent towards the apex; vein 1A does not reach the margin of the wing. The relatively very short bristles on the body and the legs and the three very small proclinate frontal bristles and the single sternopleural bristle are characteristic for *Hydromyza*. For further descriptions, see Grünberg (1910), Séguay (1934), Sack (1937), Hackman (1956), and Collin (1958).

### General behaviour

In the areas studied the flies usually occurred on the floating leaves of the nymphaeids *Nymphaea alba*, *Nymphaea candida*, *Nymphoides peltata*, but preferably on those of *Nuphar lutea*.

In spite of the fact that these insects have well-developed powers of flight they are not found at any great distance from the nymphaeids. They are difficult to capture and move restlessly around over the floating leaves, alternately walking or flying. They fly only short

Table 3. Temperature measurements in °C with a Wallacoy Universal Thermometer (GST 32; probes Ni-101x and Ni-106) in the flowers and on the floating leaves of *Nuphar lutea* and of the ambient water and air.

#### FLOATING LEAVES

Date (1977)	Tw	Ta	Tl	Tl-Tw	Tl-Ta	weather type
8-VI	16.0	18.0	19.2	3.2	1.2	sun
8-VI	16.5	18.5	19.5	3.0	1.0	sun
23-VI	—	22.6	25.4	—	2.8	sun
6-VII	24.5	28.2	29.0	4.5	0.8	sun
8-VII	23.2	24.1	25.0	1.8	0.9	bright sun
8-VII	23.4	26.1	26.5	3.1	0.4	bright sun
8-VII	23.5	25.5	25.0	1.5	-0.5	bright sun
7-VII	—	24.2	24.0	—	-0.2	heavily clouded
7-VII	—	22.0	23.0	—	1.0	clouded
29-VI	19.2	17.8	19.1	0.9	1.3	drizzle
29-VI	19.1	17.5	19.2	0.1	1.7	drizzle
29-VI	19.0	19.1	19.9	0.9	0.8	rain
29-VI	19.2	17.5	19.5	0.3	2.0	rain

#### FLOWERS

Date (1977)	Tw	Ta	Tf	Tf-Ta	weather type
8-VI	16.0	18.0	19.0	1.0	bright sun
23-VI	—	22.6	26.9	4.3	sun
23-VI	—	22.0	27.2	5.2	sun
6-VII	24.5	28.2	33.0	2.8	bright sun
8-VII	23.1	24.1	26.8	2.7	bright sun
8-VII	23.4	26.1	28.0	1.9	bright sun
7-VII	20.0	23.1	23.3	0.2	heavily clouded
7-VII	22.8	20.0	21.2	1.2	heavily clouded
7-VII	23.0	21.0	21.0	0.0	heavily clouded
29-VI	19.0	19.1	19.0	-0.1	drizzle
29-VI	19.2	17.5	18.6	1.1	drizzle
29-VI	17.2	17.8	19.1	1.3	drizzle
29-VI	19.1	17.5	17.4	-0.1	heavy rains

Tw = water temperature in °C measured 3 cm below water surface.

Ta = air temperature in °C measured 50 cm above water surface.

Tl = temperature upper surface floating leaf measured near midrib.

Tf = temperature of flower near stigma.

distances to reach other floating leaves or flowers in the neighbourhood; even when they are disturbed they make only short flights, seldom to open water or to the shore. Especially under sunny weather conditions the flies are very active on the floating leaves or in the flowers of *Nuphar* performing feeding, walking, flying, copulating, polishing, and sunning.

The nymphaeid floating leaves and flowers grow in maximum exposure to sunlight; consequently they can reach somewhat higher temperatures in comparison with water and air, as is illustrated in table 3 for *Nuphar lutea*. Such high temperatures probably stimulate the activity of the flies.

During bad weather conditions, e.g. heavy rain, they seek shelter under the aerial leaves of *Nymphaea alba* (leaves of this species often project entirely or partly above the water surface), in the flowers of *Nuphar*, or between the littoral helophytes, staying there more or less motionless.

#### Feeding behaviour

According to Eberle (1943) *H. livens* feeds in the adult stage on small insects occurring on the floating leaves of the nymphaeids, like *Hydrellia* (Ephydriidae) and Chironomidae. These small Diptera are squashed by the proboscis of this predatory fly (fig. 10) and the body fluids are consumed. On the floating leaves nearly all insects which move are attacked by *H. livens*, but only small or soft skinned insects such as Nematocera are killed.

In the laboratory ten *H. livens* specimens were kept in an aquarium with *Nuphar* leaves together with some insects, which also occur abundantly on the nymphaeids, viz., the chironomid *Cricotopus sylvestris* (Fabricius) and the ephydrid flies *Hydrellia griseola* Fallén and *Notiphila brunnipes* Robineau-Desvoidy. The chironomids and the tiny *Hydrellia* were captured and consumed by *H. livens*, the larger *Notiphila* (2.8—4.5 mm) were attacked but not harmed, while dead, squashed *Notiphila*'s were consumed.

In the areas investigated adult *H. livens* was regularly observed to occur in the flowers of *Nuphar lutea*, especially in those just opened, but never in the flowers of *Nymphaea* or *Nymphaeoides*. The flowers of *Nuphar* possess nectaria situated on the outer side of the small petals; they produce nectar containing glucose and fructose in equal amounts as could be proved with enzymatic tests. The production of nectar

occurs especially on the first day of flowering; the flower has then a strong brandy scent (Van der Velde & Brock, 1980). The flowers of *Nuphar* also have many anthers, which produce abundant pollen. Eggs of the fly *Notiphila brunnipes* and specimens of the aphid *Rhopalosiphum nymphaeae* (L.) are usually present in the *Nuphar* flowers (Van der Velde et al., 1978; Van der Velde & Brock, 1980). Because of the regular occurrence in *Nuphar* flowers the flies were suspected of obtaining food products from them. It was however difficult in the field to observe the shy flies in the flowers without disturbing them.

In the laboratory the ten *Hydromyza* specimens were offered food in the form of *Notiphila* eggs, the aphid *Rhopalosiphum nymphaeae* and moist sugar as a substitute for nectar. The flies were repeatedly observed licking the moist sugar. In most cases this behaviour continued too long to be interpreted as a mere random inspection. Further some *Notiphila* eggs and the aphids were squashed by the proboscis of the flies and consumed. Probably adult *H. livens* feeds in the *Nuphar* flowers on nectar, *Notiphila* eggs and small insects such as aphids.

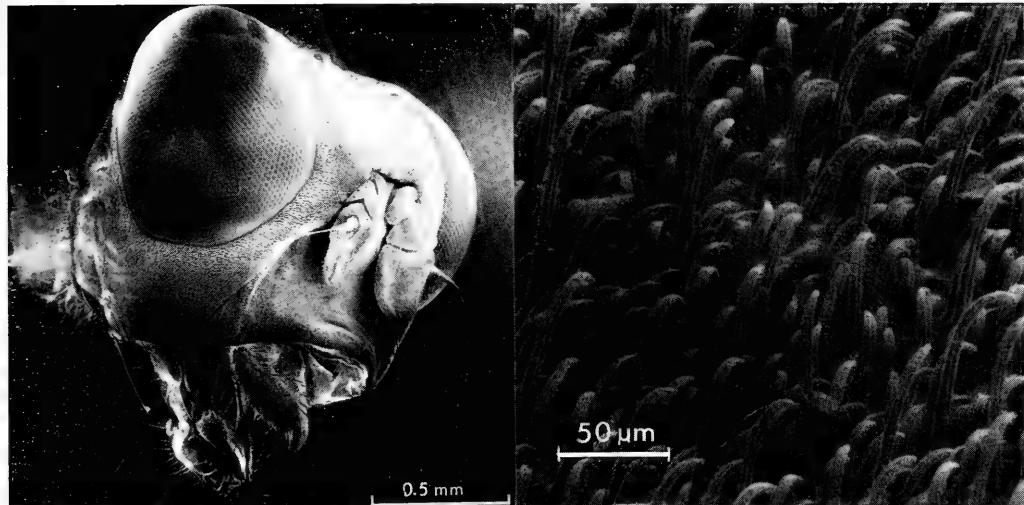
To check whether adult *H. livens* also consumes pollen, the intestines of some flies captured in *Nuphar* flowers were studied under the microscope; in the intestines diffuse material and micro-organisms could be recognized but no pollen grains.

The adult flies are numerous and it can be assumed that they play a role as pollinators of *Nuphar*. A regular flight pattern from flower to flower was never observed. However, by their regular occurrence in the flowers and by their activities, the flies certainly can cause pollination.

#### Spatial occurrence on the nymphaeids

Method. — To study the distribution of adult *H. livens* over the nymphaeid zone, floating leaves with insect-lime (see insect-lime method) were laid in transects from the littoral border vegetation to the open water (fig. 1).

Three *Nuphar* leaves were laid in the northern part of pond F; leaf 1 near the broad littoral border vegetation, consisting of *Typha angustifolia* L., *Rumex hydrolapathum* Huds. and *Scirpus lacustris* L., here the floating leaves of *Nuphar lutea* covered up to 60%; leaf 2, 6 m from leaf 1, in the centre of the *Nuphar* zone (maximum coverage 70%); leaf 3, 12 m from leaf 1, at the margin of the *Nuphar* zone with the open



10

11

Fig. 10. Scanning electron microscope photograph of the head of *H. livens*. Note the proboscis by which small preys are squashed. Fig. 11. Scanning electron microscope photograph of hydrophobic hairs on the body of *H. livens* by which the fly avoids wetting.

water, where *Nuphar* covered up to 60% of the surface.

Two leaves were laid in a narrow *Nuphar* zone at the southern side of pond F; leaf 4 near

the littoral helophyte vegetation, which borders on grassland, consisting of a narrow zone of the same plant species mentioned for the northern side, but also with *Mentha aquatica* L. (maxi-

Table 4. Absolute numbers and percentages, of adult *H. livens* and its preys caught on floating leaves with insect-lime. For the localities of the different leaves see fig. 1 and the text.

#### Absolute numbers per leaf and per taxon

Leaf number	1	2	3	4	5	6	total
<i>Hydromyza livens</i>	171	265	324	87	134	74	1,055
Nematocera spp.	359	814	2,737	734	895	599	6,138
Chironomidae spp.	227	620	2,589	663	705	463	5,267
<i>Cricotopus</i> spp.	83	288	1,790	437	358	142	3,098
<i>Hydrellia</i> spp.	346	293	137	180	154	317	1,427
	broad <i>Nuphar</i> zone			narrow <i>Nuphar</i> zone		<i>N. alba</i>	

#### Percentages per leaf and per taxon

Leaf number	1	2	3	4	5	6	total %
<i>Hydromyza livens</i>	16.2	25.1	30.7	8.2	12.7	7.0	100
Nematocera spp.	5.8	13.3	44.6	12.0	14.6	9.8	100
Chironomidae spp.	4.3	11.8	49.2	12.6	13.4	8.8	100
<i>Cricotopus</i> spp.	2.7	9.3	57.8	14.1	11.6	4.6	100
<i>Hydrellia</i> spp.	24.2	20.5	9.6	12.6	10.8	22.2	100
	broad <i>Nuphar</i> zone			narrow <i>Nuphar</i> zone		<i>N. alba</i>	

mum coverage of *Nuphar* 50%) and leaf 5 at 3 m distance from leaf 4, at the margin of the *Nuphar* zone with the open water (maximum coverage 40%).

Leaf 6, a *Nymphaea* leaf, was laid in an isolated vegetation of *Nymphaea alba*, surrounded by open water and at 6 m distance from the shore at the western side of the pond (maximum coverage of *Nymphaea* 85%).

**Results.** — The general distribution of the flies within the nymphaeid zone can be read from table 2, by comparing the results from the different leaves.

The flies appeared to have a distinctly higher abundance on the floating leaves bordering the open water (leaves 3 and 5); the lowest number of flies has been caught near the littoral helophyte vegetation (leaves 1 and 4).

Adult *H. livens* also showed a higher abundance on the broader *Nuphar* zone (leaves 1, 2 and 3) in comparison with the narrow one (leaves 4 and 5).

The lowest number of *H. livens* specimens was caught on the *Nymphaea* leaf (leaf 6), which is comparable with the *Nuphar* leaves 3 and 5 because of their similar location near the open water. This distribution suggests a preference for *Nuphar* leaves.

**Discussion.** — The higher abundance of adult *H. livens* on the nymphaeids bordering the open water may be explained by the fact that there is more food available for this predatory fly on floating leaves situated towards the open water. As mentioned before, particularly Nematocera and *Hydrellia* are food objects.

With the insect-lime method the spatial distribution of these predated insects could also be determined; the data of the most important preys are presented in table 4. When considering the spatial distribution, the absolute numbers and percentages of Nematocera and *H. livens* specimens caught on the floating leaves show the same trend. By far the largest part of Nematocera specimens is formed by the genus *Cricotopus*, mostly *C. trifasciatus* (Meigen) and *C. sylvestris* (F.). The spatial distribution of *Hydrellia* species does not show the same tendency as that of *H. livens*. The numbers of *Hydrellia* specimens on the floating leaves, however, are much smaller than those of the Nematocera (table 4).

The higher abundance of adult *H. livens* on *Nuphar* leaves in comparison with those of *Nymphaea* may be explained by the facts that the quantity of the Nematocera is relatively low

on *Nymphaea* (leaf 6, table 4) and that the females of *H. livens* deposit their eggs on *Nuphar* leaves only.

#### Sexual behaviour and sex ratio

As already mentioned adult *H. livens* resolutely approaches all insects in motion on the floating leaves. This behaviour has the function to collect food but also to find a suitable partner. The fly can be observed regularly in copulation on the floating leaves of the nymphaeids mentioned and in the flowers of *Nuphar*.

When two *Hydromyza* specimens meet, mostly they attempt to mate, resulting in copulation in the case of two adequate partners, or in a skirmish in the case of e.g. two males. *H. livens* mostly does not show an elaborate and distinct mating behaviour. Sometimes the male, during the posturing phase of mating, toddles towards the female, while repeatedly and quickly spreading the wings sideways. If the female accepts the invitation, she spreads the wings permitting the male to mount. It also has been observed that a male approached a female in a more aggressive way leading to copulation. During the insemination the females often continue feeding, polishing and even walking.

Males and females of *H. livens* can easily be separated from each other because they differ in size and in position of the genital aperture. The genital aperture is situated on the ventral side of the abdomen in the males and near the caudal tip of the abdomen in the females. Some samples from the insect-lime catch on the floating leaves were studied for calculating the sex ratio. The results are summarized in table 5. Usually more males than females were caught on the floating leaves; the percentage of males was 61.4. Maybe the males are more active, resulting in larger quantities of males in the catches with insect-lime. Another explanation might be a higher mortality of the females.

#### Deposition of eggs

As described by De Meijere (1940) and Eberle (1943), females of *H. livens* deposit eggs on the underside of the floating leaves of *Nuphar lutea*. In the study areas normally no eggs were found under the floating leaves of other nymphaeids although *Nuphar*, *Nymphaea* and *Nymphoides* locally intermingle in the same beds. Apparently the female has the ability to recognize the food plant in the presence of other nymphaeids. Only during the dry summer of 1976 eggs were found under the floating leaves

of *Nymphaea* and *Nymphoides* as well, perhaps due to the fact that the oviposition sites were strongly diminished.

Observations in the field suggest that the females inspect the floating *Nuphar* leaves before oviposition; we often observed the females walking a number of times from the leaf margin to the midrib and back again. Probably the fly in this way inspects the condition of the leaf. When a floating leaf is affected, in whatever way (even by *Hydromyza* larvae) the leaf is rejected and oviposition does not take place. From fig. 5 it can be concluded that most *Nuphar* leaves become affected by larvae of *H. livens* when the leaves have just reached the water surface. Only at the end of the season, when the numbers of adult *H. livens* are at their maximum, also older undamaged leaves (fig. 5; leaves nr. 42, 48, 81 and 65) are affected by these larvae. From these data it can be concluded that oviposition preferably takes place on just unrolled *Nuphar* leaves.

When the female has selected an adequate *Nuphar* leaf, she crawls over the leaf edge, goes into the water, and than proceeds upside down, onto the underside of the floating leaf where the egg is deposited. After approximately 20 seconds the female crawls via the leaf out of the water again and nearly immediately flies away.

Experiments in which adults were submerged showed that under such conditions the flies rise to the surface if opportunity affords, because their specific gravity is less than water. They stay under water only by clinging to a submerged object (the floating leaf). When going under water a good supply of air clings around them like a coat. The fly has a dense body-cover of small hydrophobous hairs (fig. 11). When the flies come to the surface again, they immediately lose the air coat and are apparently as dry as if they had never been under water. Because of the air coat, which they take down and the ease with which they resist wetting, oviposition can take place under water without difficulties.

A female *H. livens* deposits only one egg at a time per floating leaf. Once it was observed that a fly went down under a floating leaf on which afterwards no egg was found; when examining the underside of the leaf it appeared that a lot of periphyton occurred there, probably inhibiting oviposition.

To find out how many eggs one female of *H. livens* can deposit, a number of females were dissected and examined for eggs; 16 eggs were found at the most in the ovaries and oviducts, of

which eight eggs were in a more or less mature state.

The exact way of oviposition on the underside of the floating leaves could not be observed in the field without disturbing the flies. As already reported by Eberle (1943) (and this was also observed by us in the laboratory) the females of *H. livens*, which were kept in aquaria, did not deposit their eggs under the floating leaves of *Nuphar*. Oviposition took place above the water surface on the upper side of the floating leaves and even against the glass walls of the aquaria. These eggs, which were also deposited singly, were consumed by the adults. Probably stress caused by the imprisonment changed the oviposition behaviour.

The flies in the aquaria did not survive very long, only one or two days; they easily drowned. Probably the circumstances in the aquaria (e.g. high humidity of the air) diminished their resistance in getting wet.

Eberle (1943) pointed out that the position of the deposited eggs of *H. livens* under the floating leaves of *Nuphar* gives much information about the oviposition of the females when being under water.

In the second half of August 1979, 20 more or less undamaged floating leaves of *N. lutea* were collected in the Oude Waal. The quantity of eggs per floating leaf varied from 0 to 15. Because each female only deposits one egg under a particular leaf, more females of *H. livens* must be responsible for the number of eggs per leaf. The maximum number of eggs found by us under a *Nuphar* leaf was 29. Of 100 eggs deposited by *H. livens* on the collected *Nuphar* leaves the positions were recorded by measuring the distance to the midrib and the petiole (attachment place to leaf blade). In fig. 12 the positions of these eggs are projected on a single floating leaf of *Nuphar*. The graph of fig. 13 shows the distance between these eggs and the midrib of the *Nuphar* leaf measured along the longitudinal axis of the eggs.

According to these data and those of Schütte (1921) and Eberle (1943) several regularities in the positions of the eggs appeared to exist, viz.:

(a) The broad rostral end of the egg is situated mostly towards the midrib. In dissected females the more pointed caudal end of the egg lies more towards the oviduct, during oviposition this end leaves the abdomen before the broader end. During oviposition, therefore, the female must be directed with her head towards the midrib.

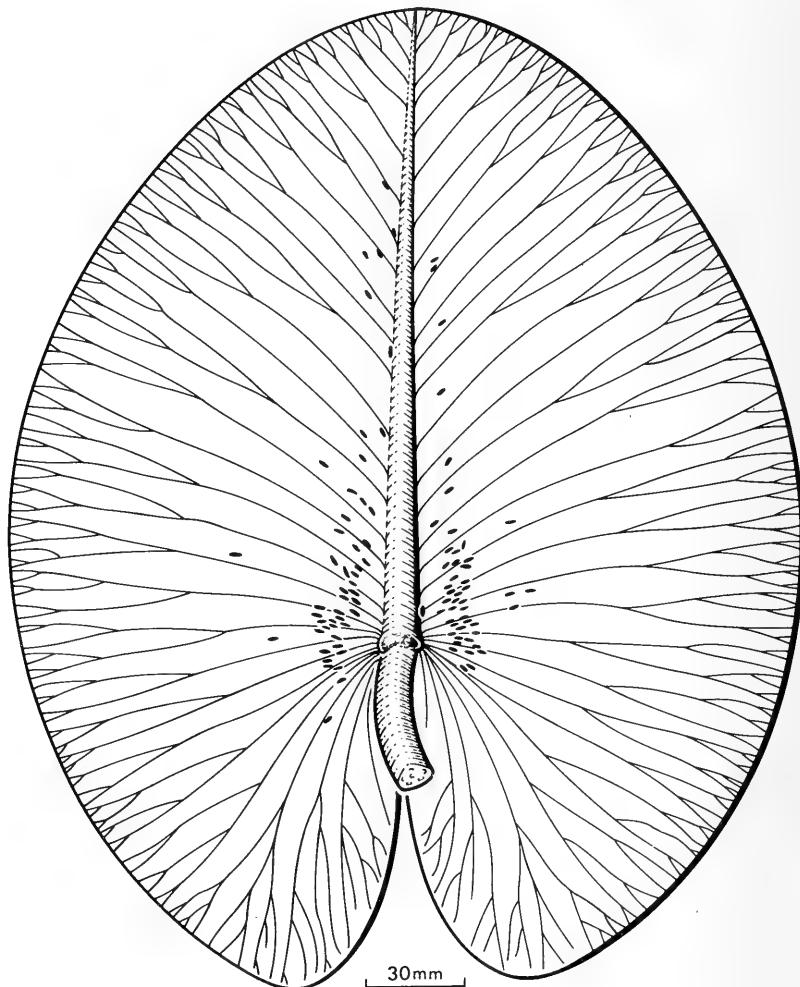


Fig. 12. The positions of 100 eggs of *H. livens* (collected from 20 leaves) projected on the underside of a single *Nuphar* leaf.

(b) The longitudinal axis of the egg is mostly situated parallel to the lateral leaf nerves, mostly between two of them.

(c) Most of the deposited eggs can be found near the basis of the midrib.

(d) Most of the eggs are deposited approximately 7—10 mm from the midrib (fig. 13).

From these data it can be concluded that a female of *H. livens* mostly crawls into the water via the edge of the broadest part of the floating leaf where the lateral nerves are dichotomously branched. When under water, clinging upside down to the leaf and covered with an air coat, the female crawls towards the midrib, guided by

a lateral leaf nerve, which is translucent. Probably the visual observation or touching of the midrib is a strong stimulus for oviposition because the distances between the eggs and the midribs mostly were approximately the length of the flies. These conclusions agree with those of Eberle (1943).

#### Spatial occurrence of egg deposition

In order to find out where egg deposition mostly takes place within the nymphaeid zone, both in the Oude Waal and Haarsteegse Wiel, in 1977 regularly 15 floating *Nuphar* leaves were collected at random at three sites, viz., 15 near

the littoral border vegetation, 15 in the middle of the *Nuphar* zone and 15 near the open water. Leaves were collected every month from May until September in the Oude Waal and every two weeks from June until September in the Haarsteegse Wiel. The eggs and larvae occurring under and in the leaves were counted per site per date.

In the Oude Waal in total 62 larvae and eggs were counted on the leaves bordering the littoral helophyte vegetation, 38 on leaves from the middle of the *Nuphar* zone and 65 on floating leaves from the location near the open water.

In the Haarsteegse Wiel, in total 81 larvae and eggs were found on the leaves near the littoral border vegetation, 79 on leaves from the middle of the *Nuphar* zone and 94 on leaves bordering the open water.

It can be concluded that oviposition in the Oude Waal takes place more often under leaves at the two edges of the *Nuphar* belt than under leaves in the middle of the *Nuphar* zone. The results from the Haarsteegse Wiel show this trend less clearly.

From the data obtained with the insect-lime method it appeared that the adults were definitely more abundant on the nymphaeids bordering the open water because of the higher abundance of food organisms there. The large number of eggs and larvae under and in floating leaves of the sites near the open water can be explained in this way. The high frequency of egg deposition under floating leaves bordering the littoral helophytes may be explained by the fact that wind and wave action are less pronounced here.

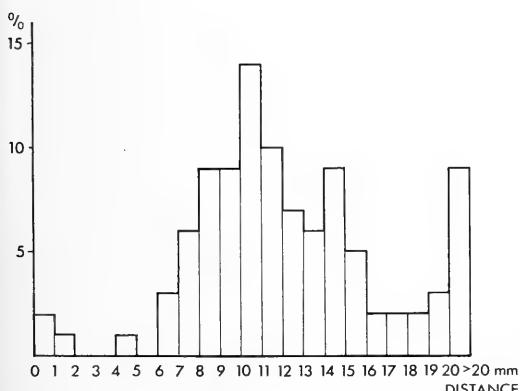


Fig. 13. The distances of 100 eggs of *H. livens* to the midribs of the floating leaves on which they were deposited, measured along the longitudinal axis of the eggs (see also fig. 12).

## Mortality and predation

As may be concluded from fig. 6, the numbers of adult *H. livens* decrease at the end of the growing season of *Nuphar*. The mortality of adults may have several reasons, e.g. falling temperatures, diminishing of the floating leaf area (figs. 5, 6 and 7) and lack of food (table 2). Exhaustion of females and risks under water during oviposition, such as predation by fish, might also cause mortality; the sex ratio data mostly showed a majority of males (table 5). After heavy rain the population size of adult *H. livens* seems to be diminished. Although the flies have hydrophobous hairs, they easily drown when their skins become wet. Probably a long-lasting contact with water or even very humid conditions (aquaria) diminish their resistance against getting wet. Predation on adult *H. livens* has never been observed by us. However, Odonata, swifts (*Apus apus* (L.)), swallows (*Hirundo rustica* L., *Delichon urbica* (L.)), terns (*Sterna hirundo* L., *Chlidonias niger* (L.)) and the Green frog (*Rana esculenta* (L.)) prey on the insects from the floating leaves and thus can occasionally catch *H. livens*.

## THE EGG

### Morphological description

The eggs of *H. livens* have a length of 1.9—2.0 mm and a width of 0.5—0.6 mm. Freshly laid eggs are yellow-white in colour, a few hours before hatching they become darker. The eggs have the appearance of a boat (fig. 14a), with differently shaped ends: the caudal end is bluntly pointed, while the broader rostral end is more rounded and contains the micropyle. A straight, acute carina extends longitudinally from end to end and runs medially along the bottom of a rather deep, broad, longitudinal fossa (fig. 14b), dividing it into two similar parts. This divided fossa is laterally bordered by two other longitudinal carinae, which run almost parallel to the median carina, converging and uniting with the ends of the egg. The eggs are always deposited singly under the floating leaves of *Nuphar* and are firmly fixed to the substrate so that it is nearly impossible to separate them from a floating leaf without damage to the chorion or the leaf tissue. Apparently a small amount of sealing fluid accompanies the egg at oviposition causing the firm attachment to the floating leaf.

Eggs have been studied by means of scanning

Table 5. Sex distribution and the percentage of males in samples of *H. livens* caught with insect-lime.

Date (1977)	Number of specimens examined	Males	Females	percentage of males
30-VI	2	1	1	50.0
12-VII	13	11	2	84.6
21-VII	19	12	7	63.2
28-VII	7	3	4	42.9
5-VIII	25	13	12	52.0
12-VIII	24	6	18	25.0
25-VIII	125	82	43	65.6
1-IX	91	63	28	69.2
8-IX	5	0	5	0
Total	311	191	120	61.4

electron microscopy; in this way the external and internal appearance of the chorion could be studied (fig. 14). The external surface of the chorion, especially near the carinae, appears more or less reticulate, being composed of polygonal units (fig. 14b). The reticulation is elongated in the direction of the long axis of the egg and within the netlike structures many pores can be recognized (fig. 14b and 14c).

To study the internal structure of the chorion the eggs were sliced with a razorblade and examined with the scanning electron microscope (fig. 14d, e and f). The chorion appeared to possess cavities, which are apparently in contact with the pores in the external walls. The chorion is distinctly thicker at the carinae and the depression between them than on the lateral sides, as shown in fig. 14d.

#### The function of the chorion

The chorion protects the eggs against certain predators but also can function as a plastron. According to Hinton (1967, 1971) the terrestrial eggs of the majority of insects have structures in the chorion which have the function to hold air to maintain respiration on becoming wet, e.g. by a rain shower; the chorion of many aquatic and semi-aquatic eggs is solid.

It appears from the scanning electron micrographs (fig. 14) that the chorion of the aquatic egg of *H. livens* contains cavities. These cavities possibly hold an air layer which functions as a plastron. Hinton (1960) has shown that a system of hydrofuge structures in the chorion can form the architecture for a permanent, unshrinkable, physical gill, a plastron. An egg with a plastron can remain immersed indefinitely and

obtains the oxygen it requires from the ambient water, provided that the water is well-aerated.

Normally the eggs of *H. livens* are deposited under the floating leaves of *Nuphar* so during their development into larvae they are immersed in the extreme upper layer of water. In natural habitats, such as the Oude Waal, the water under the floating leaves is well-aerated. On 25 August 1977 the amount of oxygen in the water of the Oude Waal was measured with an oxygen meter (Y.S.I. model 151A). Directly under the floating *Nuphar* leaves the measured oxygen saturation percentage was 78%. At depths of 50, 100 and 150 cm (near the bottom) the oxygen saturation percentages diminished and were 75, 70 and 45% respectively.

Eggs with a plastron are able to survive under the floating leaves because of the well-aerated conditions.

In the laboratory, eggs of *H. livens* normally developed into larvae when floating leaves with eggs were kept floating in aquaria and also, when they were kept under very humid conditions outside the water. The eggs, however, soon desiccated when floating leaves with eggs were kept in a dry environment outside the water. Also when floating leaves with eggs were kept on the bottom of an aquarium, 20 cm below the water surface in non-aerated water, the eggs had not yet hatched when the leaves had already decayed; probably the eggs did not develop because of depletion of oxygen. It can be concluded that the eggs develop in well-aerated water or in very humid air; the chorion, however, is not adapted to prevent desiccation and probably forms the architecture for a physical gill or plastron.

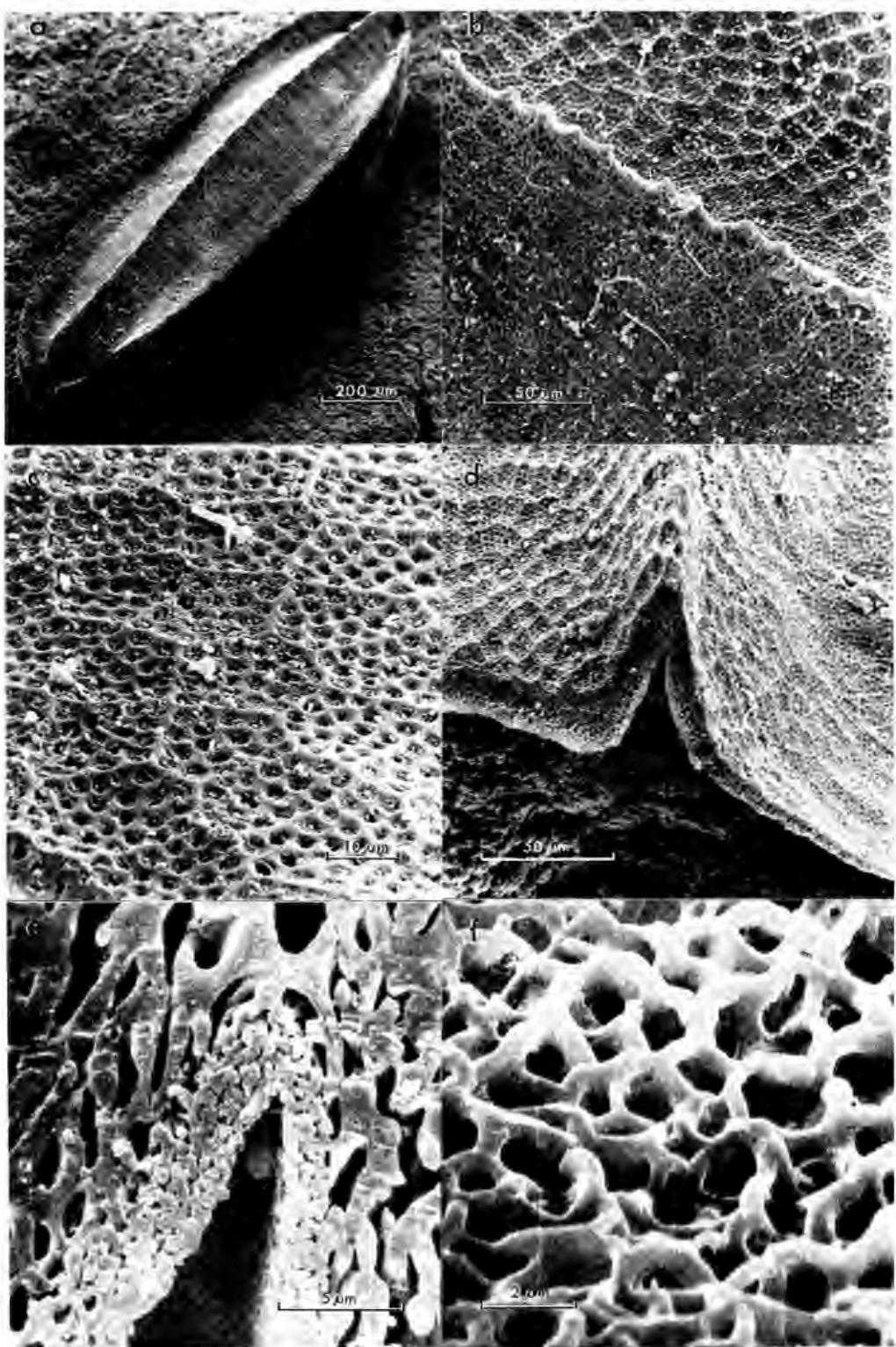


Fig. 14. Scanning electron microscope photographs of the egg stage of *H. livens*: (a) overall view, note the micropyle at the frontal end; (b) detail of the chorion near the median carina; (c) detail of the chorion showing polygonal units and pores; (d) transversal section, showing the internal structure of the chorion near a carina; (e) detail of the internal structure of the chorion, showing many pores and cavities; (f) detail of the inner side of the chorion also showing pores.

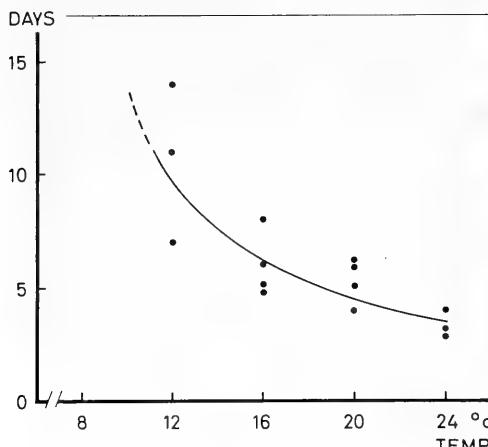


Fig. 15. Duration of the development of *H. livenes* eggs into larvae in relation with temperature.

#### Development in relation to temperature

Eberle (1943) already discussed the fact that the development of eggs into larvae is dependent on temperature. In spring, when the water is relatively cold, the duration of the development can last out up to two weeks, while in summer, when the water is warmer, the larvae hatch after 3 to 4 days after the time of egg deposition (Eberle, 1943).

It is difficult to study the development of the eggs in relation to temperature under controlled circumstances because it is difficult to obtain enough eggs of the same age which are freshly deposited by the females of *H. livenes*. As already discussed one can only sporadically observe the oviposition in natural habitats, while the flies in captivity do not deposit their eggs in the normal way under the floating leaves. In order to obtain eggs which were more or less of the same age, 25 undamaged, young leaves of *Nuphar*, under which no eggs were deposited, were marked in the Oude Waal at the end of August 1979. After 24 hours these leaves were collected and 19 eggs of *H. livenes* were obtained from them. The differences in age of these eggs could be 24 hours at most; the temperature of the Oude Waal water was at that time 18 °C. In the laboratory the floating leaves with eggs were kept in aquaria and placed in different climate chambers which had constant temperatures of 8, 12, 16, 20 and 24 °C. Temperatures within this range had also been measured in the Oude Waal (fig. 6). In the climate chamber of 8 °C three eggs were placed, in the other cham-

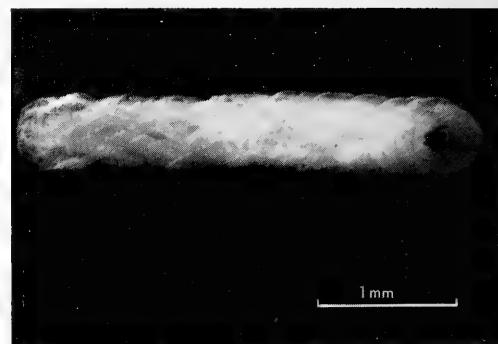


Fig. 16. Photograph of a *H. livenes* larva sampled from a leaf blade.

bers four each. By daily observations the development of the eggs into larvae was followed (see fig. 15).

The data thus obtained confirm that the development of the eggs is indeed dependent on temperature and that the development goes faster at temperatures which are normally measured in summer in comparison with colder circumstances in spring and autumn. Below a certain temperature, between 8 and 12 °C, the eggs do not develop at all into larvae. The large differences in developmental rate of the eggs, especially in the climate chambers of 12 °C and 16 °C, are probably caused by the way the eggs were obtained, viz. at a temperature of 18 °C.

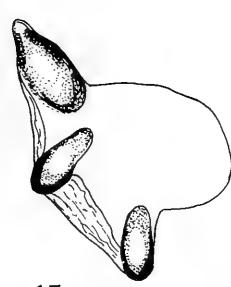
#### THE LARVA

##### Morphological description

The larva of *H. livenes* (fig. 16) is yellow-white in colour with the exception of the black cephalopharynx skeleton (fig. 18), the brown, kidney-shaped, frontal stigmata and the dark terminal stigmata (fig. 17).

The anterior stigmata consist of short processes, each with several buds; the total number of buds on one stigma being about 200 (De Meijere, 1895). According to Schütte (1921) there is no difference between the number of stigmatic buds of larvae and pupae of the different generations. In the summer larvae (in our case the first and second generation) the diameters of these buds are smaller, however, than in the winter larvae (in our case the third generation). The anterior stigmata are not yet visible on freshly hatched larvae.

In the translucent body the long, green intestine, the main tracheae and the very well devel-



17



18

Fig. 17. Terminal stigmata (spiracular disc) of a *H. livens* larva. Fig. 18. Cephalopharynx skeleton of a larva of *H. livens*.

oped salivary glands are visible. The digestion tract of the full-grown larva is at most 8.5 cm long (about eight times the total length of the larva) (Schütte, 1921).

The body is cylindrical and elongate, and consists of 12 more or less visible segments. Some intersegmental grooves are very distinct. The anterior end of the body is moderately rounded with the exception of the acute, emergent teeth of the cephalopharynx skeleton. Posteriorly, the body is bluntly tapering to the more or less rounded or acute chitinous projections of the terminal stigmata (fig. 17).

The integument is covered with pointed, chitinous projections which are directed backwards. These projections are rather uniform in

size and shape over the body except on the anterior margin of the first thoracic segment, where they are larger and more distinct. On the younger larvae, bristle-like projections can be recognized above the mouth-hooks. In fig. 19, scanning electron microscope photographs of heads of larvae of *H. livens* are presented. The larva of fig. 19a was collected from a floating leaf of *Nuphar lutea* and was 2–3 days of age. The larva of fig. 19b was collected from a petiole of a floating *Nuphar* leaf and is a few days older.

According to Schütte (1921) the larvae of the summer generation measure 9.5 mm in length at a width of 2.5 mm, while the length and width of larvae of the last generation measure 11 and 3

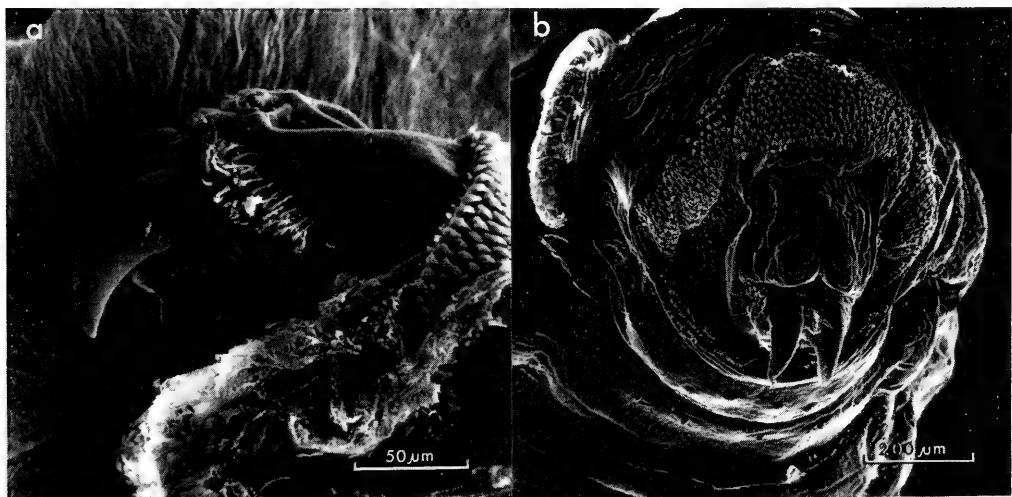


Fig. 19. Scanning electron microscope photographs of the heads of two *H. livens* larvae, sampled from a leaf blade (a) and from a petiole (b).

mm, respectively. According to Eberle (1943) full-grown larvae of the first generation measure 9 mm in length, while the mature larvae of the last generation can reach a length of 11 mm.

In the Oude Waal full-grown larvae of the last generation were 10.5—13.0 mm in length, with a width of 1.5—2.5 mm.

According to Schütte (1921) there are four

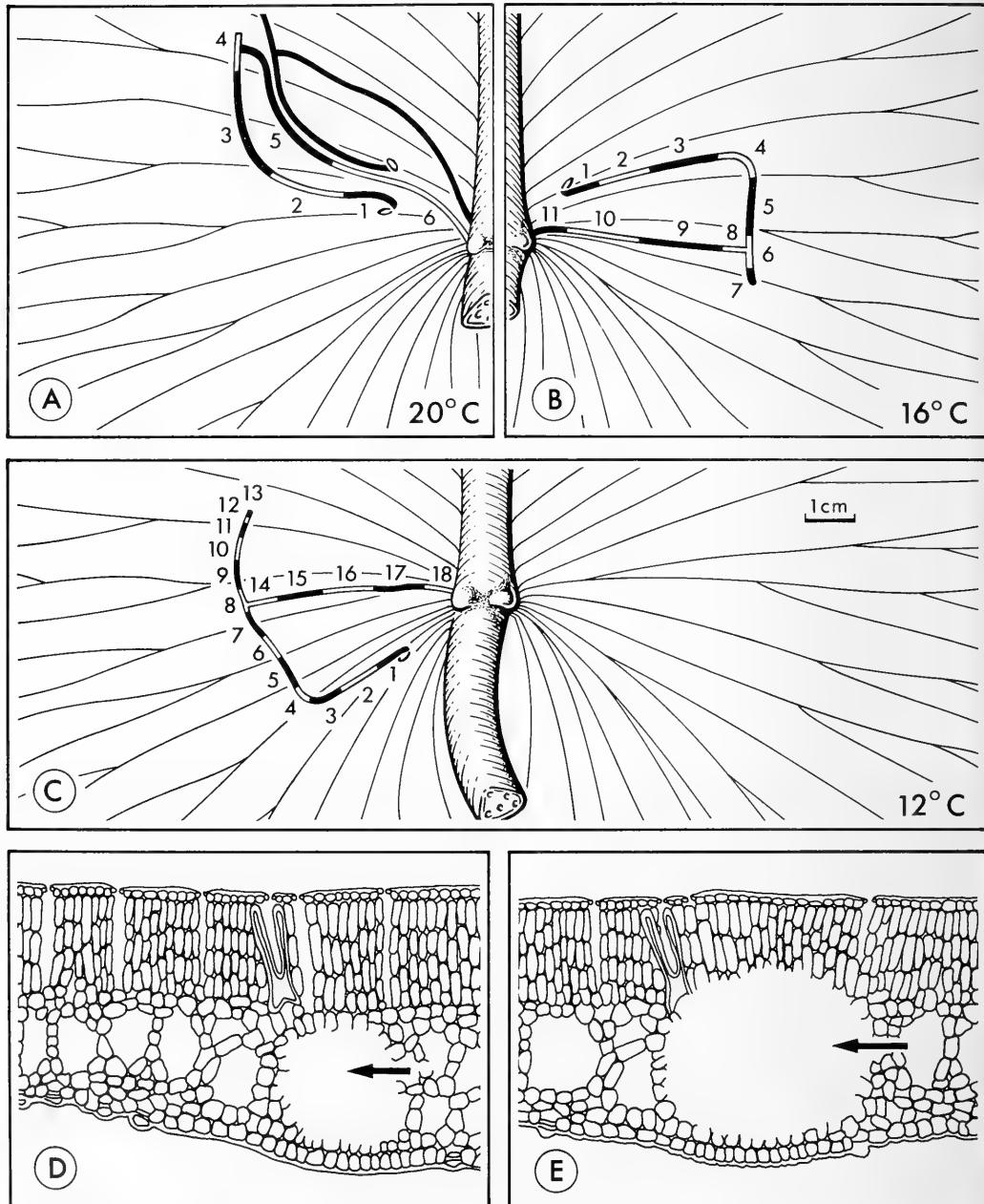


Fig. 20. Daily length increase of mine tracks of three *H. livens* larvae in *Nuphar* leaves at a temperature of 20 °C (A), 16 °C (B) and 12 °C (C), respectively. Each number corresponds with a day. Transversal section of a part of a *Nuphar* leaf with a mine track (arrow) of a just hatched larva (D) and an older larva (E) in the leaf blade.



Fig. 21. Photograph of a part of a *Nuphar* leaf with mine tracks of *H. livens* larvae.

instars; this author also gives an extensive anatomical description of the larva and its way of nutrition.

#### The process of hatching from the egg

Shortly before the time of hatching, the egg becomes darker in colour, indicating that the larva within the egg is fully developed. The place of emergence of the larva through the egg shell is very constant. With the aid of relatively large, acute, chitinous mouthparts the larva makes an exit through the egg shell on the side next to the leaf. The position of the exit hole is determined by the position of the larva in the egg. So the exit is made near the blunt, broad, rostral end of the egg, which is mostly directed towards the midrib of the floating leaf. Via this hole the larva bores directly through the lower epidermis into the mesophyll of the floating *Nuphar* leaf. After the process of hatching the empty egg shell remains sticking to the leaf, closing off the exit, so that water is not able to enter the mine gallery in the leaf.

#### General feeding behaviour

In the investigated areas the larvae of *H. livens* feed on the floating leaf and petiole tissue of *Nuphar lutea*. During the early period of feeding only the spongy parenchyma of the floating leaf is consumed, while in a later stage, when the larva has increased in volume, also the palissade parenchyma of the mesophyll is eaten (fig. 20d and 20e).

While eating through the floating *Nuphar* leaf the larva produces a mine gallery in it, and afterwards also in the petiole where the larva eats itself spirally downwards (fig. 21 and fig. 22c).

With the aid of the large acute mouth-hooks

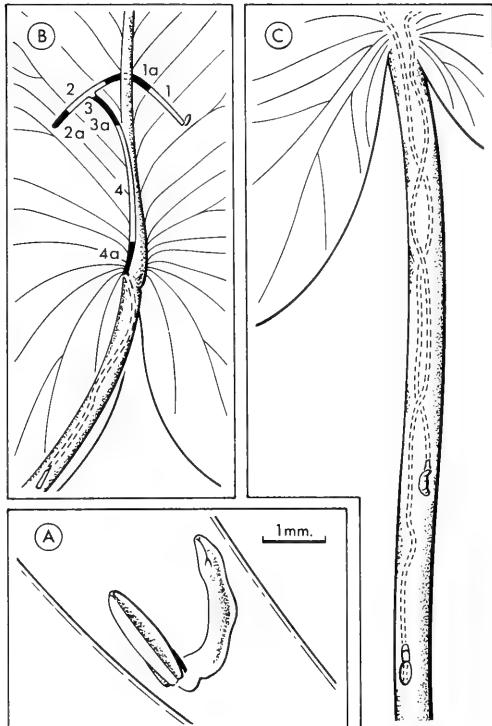


Fig. 22. (A) Just hatched larva of *H. livens* in its mine track and the empty egg shell. (B) Larval consumption by day (white) and by night (black and marked with a) in a *Nuphar* leaf. (C) Mine tracks of *H. livens* in a petiole of a *Nuphar* leaf. (Modified after Eberle, 1943.)

the larva loosens the plant cells while making mowing movements with the head. According to Schütte (1921) the larvae of *H. livens* secrete digestion enzymes which dissolve the plant cells before they are ingested. Consequently one can find no recognizable fragments in the intestines of the larvae.

In the floating leaves and petioles of *Nuphar* many sharp, hair-like branched trichosclereids occur which consist of calcium oxalate. The secreted digestion enzymes also dissolve these sharp trichosclereids; the intestines of the larvae are not harmed by them in this way. The calcium oxalate is transformed into calcium carbonate in the Malpighian organs (Schütte, 1921).

Eberle (1943) already demonstrated that the larva of *H. livens* feeds by day and by night, as is illustrated in fig. 22b. The larval consumption and consequently the length of the mine is somewhat larger by day than by night, probably due to differences in temperature between day and night.

### Regularities in larval feeding and mine patterns

According to Schütte (1921) the larvae are negatively phototactic, which may help and guide their position in the leaf tissue. According to Eberle (1943) and to our own observations the way of larval feeding shows regularities, viz.:

(a) The larva, which has recently left the egg, mostly creates a mine gallery that makes a sharp bend of approximately 180° (fig. 22a).

(b) After that the larva mostly mines in the direction of the leaf margin, more or less parallel to the lateral leaf nerves. When eating towards the leaf edge, the thickness of the mesophyll decreases while the volume of the larva in-

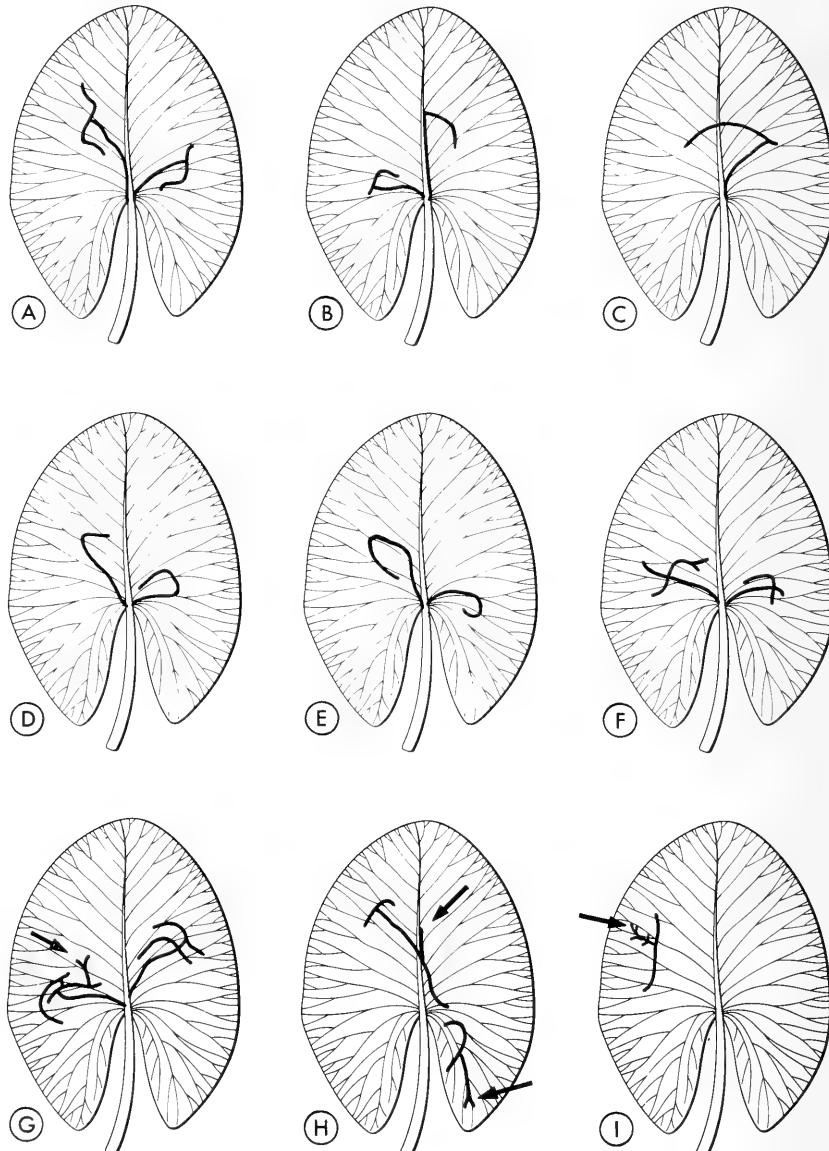


Fig. 23. Various types of mine tracks of larvae of *H. livenes* in leaves of *Nuphar lutea*. The arrows show the locations of dead larvae.

creases; this results in a more or less sharp gradual bend of the mine gallery parallel to the leaf margin (fig. 23a—e).

(c) After this the feeding behaviour of the larva suddenly changes. This change is correlated with the first moulting period of the larva. After having cast the old skin, the larva mines more or less at right angles to the previously created part of the mine gallery in the direction of the midrib or petiole of the floating leaf (fig. 23a—e).

(d) On reaching the petiole the larva mines spirally downwards where ultimately the full grown larva pupates.

These regularities in larval feeding behaviour cause regularities in the shape of the mine galleries and consequently one can distinguish certain mine types, in the leaf blades, viz.:

(1) The T-shaped mine gallery (fig. 23a, b and c). This type is created by larvae which after the first moulting period crawl backwards in the older part of the mine gallery before starting to eat in the direction of the midrib or petiole.

(2) The arch-like mine gallery (fig. 23d and e). In this type, the larva does not crawl backwards after moulting.

(3) The cross-like or irregularly shaped mine gallery (fig. 23f, g, h, i). This type of mine gallery is the result of disturbances in the mining behaviour of the larva, or it is caused by the damaged state of the leaf blade. Although the eggs of *H. livens* are mostly deposited under young and undamaged floating leaves, these leaves might be damaged before the eggs have hatched. This damage on the leaves of *Nuphar lutea* might, for instance, be caused by the feeding by the Coot (*Fulica atra* L.), the gastropod *Lymnaea stagnalis* (L.), the beetles *Donacia crassipes* F. and *Pyrrhalta nymphaeae* (L.), the caterpillar *Nymphula nymphaeata* (L.), but above all by other *H. livens* larvae. When the floating leaf is not damaged too much, the younger larva has the ability to avoid the older affected leaf part (fig. 20a).

When the larval numbers are at their maximum, there is a great chance that a larva of *H. livens* crosses an older mine gallery. In that case the larva sometimes crosses the mine under a right angle but mostly the larva makes use of the older gallery for a while (fig. 23g). This can result in creeping into wrong directions of the larva, and, consequently, in an irregular shape of the mine gallery. It also happens that a larva mines in the wrong direction after the first moulting (fig. 23h, i) also resulting in an irregu-

lar shape of the mine gallery in the leaf blade.

In order to get an idea of the occurrence of the different types of mine galleries, 34 floating leaves were collected in the Oude Waal on 11 September 1979. In total, 207 mine galleries could be recognized in these leaves. Of the mines 60.5% could be classified within the T-shaped type, 30.5% in the arch-like type, and 9.0% in the cross-like or irregular shaped type.

#### Feeding behaviour and temperature

In the laboratory the larval consumption in floating leaf blades was followed in different climate chambers.

In fig. 22b the larva has reached the petiole on the 4th day. This also happened with a larva in the laboratory in the climate chamber of 24 °C. In the climate chamber of 20 °C a larva reached the petiole on the 6th day, while at constant temperatures of 16 °C and 12 °C this happened on the 11th and 18th day after the moment of hatching from the egg, respectively. The daily consumption of the three larvae in the climate chambers of 20 °C, 16 °C and 12 °C was followed in detail (fig. 20 and table 6).

Although the consuming activity of only a few larvae was followed under controlled cir-

Table 6. Daily length increase of mine tracks in mm of three *H. livens* larvae in leaf blades of *Nuphar* at temperatures of 20, 16 and 12 °C, respectively.

Number of days	20 °C mm	16 °C mm	12 °C mm
1	12	8	7
2	16	10	8
3	23	11	7
4	8	9	6
5	32	13	7
6	34	7	6
7	—	2	7
8	—	5	4
9	—	17	5
10	—	15	6
11	—	7	4
12	—	—	1
13	—	—	1
14	—	—	5
15	—	—	8
16	—	—	11
17	—	—	10
18	—	—	5
Total length of mine track	125	104	108 mm
Mean length per day	20.8	9.5	6.0 mm

cumstances one can draw some general conclusions from the data thus obtained. The consuming activity is temperature dependent and apparently the development rate is faster under warmer conditions during the summer, than in spring and autumn when colder air and water temperatures occur.

The daily consumption of the larvae is not constant at a constant temperature. Generally the larvae consume more when they become older, only during the moulting period the larval consumption is very low (fig. 20, table 6).

Also the time needed for moulting seems to be temperature dependent and consequently takes a longer time under colder circumstances.

#### Differences in consumption and feeding behaviour between the generations

According to Schütte (1921) and Hendel (1928) the length of the mine galleries in the

petioles of the summer and winter pupae is ca. 10 cm and 20—25 cm respectively. In order to get an impression of the larval consumption of plant tissue of the various generations both in the second half of July and in September, 1977, a number of floating leaves and leaf stalks of *Nuphar* were gathered in the Oude Waal. The lengths of 25 mine tracks in the leaf blades and another 25 in the leaf stalks were measured (table 7).

The measurements of July, 1977, correspond with the second generation of *H. livens*. This generation, as well as the first one, completes its life cycle within one growing season of *Nuphar*. The lengths of the mine galleries measured in September correspond with the third generation, which generation hibernates as pupa.

Three stages of the mine track have been distinguished in the floating leaf and petiole, viz.:

(1) mine stage 1; this stage corresponds with

Table 7. Lengths of 25 mine tracks of *H. livens* larvae in leaf blades and petioles of *Nuphar*, in July and September, 1977. For explanation of the mine stages, see the text.

July, 1977

n	Mine stage 1 in mm	Mine stage 2 in mm	Total length in leaf blade (mm)	Mine stage 3 in petiole (mm)
1	37	27	64	37
2	34	84	118	36
3	25	76	101	29
4	33	33	66	48
5	34	35	69	38
6	24	36	60	32
7	52	51	103	29
8	38	59	97	39
9	31	36	67	38
10	30	116	146	29
11	39	104	143	54
12	53	65	118	40
13	38	48	86	30
14	41	55	96	84
15	40	63	103	58
16	54	79	133	41
17	41	50	91	40
18	48	35	83	42
19	57	68	125	71
20	60	207	267	49
21	49	61	110	41
22	62	75	137	44
23	40	55	95	43
24	41	56	97	35
25	38	39	77	39
mean length	41.6	64.5	106.1	42.6
SD	± 10.3	± 36.9	± 41.8	± 12.9

(Continued on page 85)

the consumed length of the mine gallery before the first larval moulting period in the leaf blade;

(2) mine stage 2; this stage corresponds with the consumed length of the mine gallery in the leaf blade after the moulting of the larva;

(3) mine stage 3; the length of the mine gallery in the petiole.

The results of the measurements are summarized in table 7. The differences in the mean length of the mine galleries in the leaf blade between the second and the third larval generation of *H. livens* are not large. The differences in mean length of the mine galleries in the petioles, however, are very conspicuous between these generations with mean lengths of  $42.6 \pm 12.9$  and  $95.1 \pm 28.3$  mm, respectively. Therefore, the total length of the mine and consequently the consumption of plant tissue of the generation that completes its life cycle within the growing season of *Nuphar* is smaller than that of the one which hibernates as pupa during the next winter. Apparently the generation that hi-

berates needs more energy to survive this cold period.

Also the feeding behaviour of the first and second generation differs from the third one, in the Oude Waal. Schütte (1921) and Eberle (1943) already recorded that the fullgrown larvae of the first generation construct a provision for the emergence of the adults in the form of a window. In constructing this window the fullgrown larva eats towards the exterior of the petiole until it reaches the epidermis. Here it removes all surrounding tissue from a more or less circular area with a diameter of 2–3 mm, which is destined to be the window and is composed of the epidermis only. The window is only large enough to allow the passage of the emergent adult. In the Oude Waal the fullgrown larvae of both the first and second generation construct such a provision.

According to Eberle (1943) and according to our own observations the fullgrown larvae of the last generation (in our case the third one) do

(Continuation from page 84)

September, 1977

n	Mine stage 1 in mm	Mine stage 2 in mm	Total length in leaf blade (mm)	Mine stage 3 in petiole (mm)
1	50	64	114	90
2	59	78	137	88
3	41	90	131	75
4	42	55	97	80
5	41	62	103	73
6	55	75	130	93
7	37	42	79	101
8	35	120	155	80
9	48	61	109	80
10	42	50	92	86
11	51	66	117	102
12	40	155	195	94
13	45	52	97	76
14	57	55	112	90
15	50	77	127	78
16	51	60	111	72
17	47	71	118	116
18	59	82	141	75
19	35	121	156	124
20	60	75	135	74
21	34	41	75	80
22	46	35	81	88
23	39	74	113	197
24	35	61	96	150
25	47	73	120	116
mean length	45.8	71.8	117.6	95.1
SD	$\pm 8.1$	$\pm 26.9$	$\pm 27.0$	$\pm 28.3$

not construct windows for emergence. When they have pupated they stay as long as possible in the petioles, in the broadened end part of the mine gallery.

### Mortality

Predators of the larvae of *H. livens* were never observed. The floating leaves and petioles of *Nuphar* not only provide the larvae with food and oxygen, but also with protection against possible predators.

As already discussed a damaged state of the floating leaf can cause irregularities in the mining behaviour of the larvae, resulting in their death (fig. 23g). Also when the larvae mine in wrong directions they die before pupation (fig. 23g, h). When a particular floating leaf is affected by various larvae of *H. livens*, the leaf becomes too much damaged causing a faster rate of decomposition. The larvae, which have not reached the petiole in time drown, die because of lack of fresh plant tissue, or become infected by fungi. When too many larvae reach a particular petiole and consume too much tissue the leaf stalk easily breaks off or decomposes too fast. Then only the larvae which arrived first in the petioles, and which have eaten themselves a longer way downwards survive.

An important factor of mortality is the intra-specific competition especially at the end of the season when the number of larvae is maximal and more larvae mine in the same floating leaf.

In the last week of August, 1977, 25 floating leaves of *Nuphar* which were affected by *H. livens* larvae were gathered in the Oude Waal; the mean number of mine tracks per floating leaf was four. At the end of September, 1977, 25 leaf stalks of affected leaves were gathered and in them 1—3 pupae were found with a mean number per leaf stalk of two. So in 1977 about 50% of the larvae of the last generation did pupate, while apparently the other 50% died because of competition, especially with the older larvae. On 11 September, 1979, the mean number of mine galleries per floating leaf was 6 (maximum 15) (34 affected leaves from the Oude Waal were examined). On 15 October, 1979, 20 leaf stalks were gathered and in them 32 pupae were found. The maximum number of pupae per petiole was three, while the mean number per leaf stalk was 1.6. Therefore, in 1979 less than 1/3 of the larval population of the third generation in the Oude Waal pupated.

It can be concluded that the petiole offers room to 1—3 pupae only. Schütte (1921) re-

corded that the mine tracks of the larvae in the triangular petioles are mostly situated in their edges, using the space optimally in this way.

### Pupation

According to Schütte (1921) the metamorphosis of summer larvae into summer pupae takes only a short time; transitional stages were never found. The metamorphosis of larvae into winter pupae, however, takes a period of at least 8—10 days.

The process of metamorphosis starts after the 4th moulting period. Just before pupation the larvae excrete calcium carbonate via their digestive tracts and originating from the Malpighian organs. A clod of calcium carbonate can be found near the caudal parts of the pupae in the petioles (fig. 24).

During the pupation of the winter generation the skin becomes ca. 9 times thicker by the formation of chitinous layers; furthermore calcium and silicium are chemically bound to chitine and thus incorporated in the pupal skin (Schütte, 1921).

### THE PUPA

#### Morphological description

The pupae which emerge within the growing season of *Nuphar*, according to Schütte (1921) and Eberle (1943) summer pupae (in the Oude Waal and Haarsteegse Wiel the first and second generation), measure 7.0—8.3 mm in length

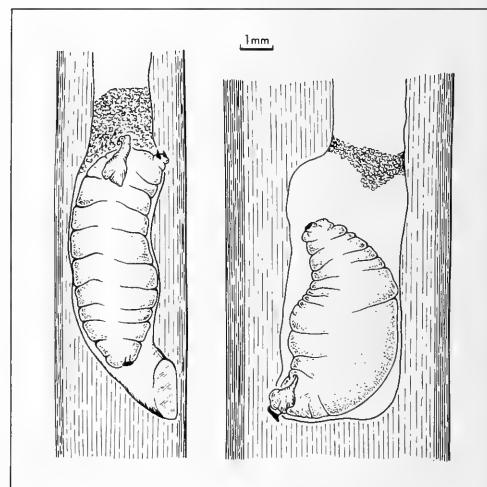


Fig. 24. Positions of a summer and a winter pupa in the petioles of *Nuphar* leaves (Eberle, 1943).

with a width of 2.6—3.3 mm ( $n = 10$ ). Their pupal skin is rather soft, yellow-brown in colour and more or less translucent so that the developing adult is to be seen. The cylindrical body mostly consists of 12 clearly visible segments, while a large amount of minor chitinous projections on the pupal skin gives it a faintly, transversally striated appearance. The kidney-shaped frontal stigmata and the acute projections of the terminal stigmata are brown-black in colour and thus can be easily recognized.

The pupae of the third generation, according to Schütte (1921) and Eberle (1943) winter pupae, which hibernate during the winter, measure 6.2—7.2 mm in length at a width of 3.4—4.1 mm, so they are shorter but more robust than those of the first and second generations (fig. 24). The pupal skin is stout, yellow-brown to brown-black in colour and not translucent. The thick-set body, on which the 12 segments are not all clearly visible, has on its dorsal side a more or less visible yellow-brown line running from the kidney-shaped anterior stigmata to the large, dark-brown, acute projections of the terminal stigmata. The skin is also faintly transversally striated (fig. 25).

In the summer pupae the thoracic stigmata are in connection with the anterior stigmata of the pupal skin. This is not the case in the winter pupae; here the anterior stigmata of the pupal skin are in connection with a well-developed air layer, ca. two times as large in the winter pupae as in the summer pupae (Schütte, 1921).

#### Position of the pupae in the leaf stalks

Eberle (1943) already described that the pupae of the first generation have an other position in the petiole than the pupae which have to hibernate (fig. 24). The pupa which emerges within the growing season of *Nuphar* (the first and second generation in our case) is situated in a small room in the leaf stalk with its rostral end below and its caudal end above. This rostral end faces the window, the provision for the emergence of the adult, while the acute projections of the terminal stigmata are stuck into the living tissue of the leaf stalk. The room in which the pupa matures is closed off from the remainder of the mine gallery by a plug of loosened plant cells.

The pupa of the last generation (in our case the third one) is situated in a larger room in the petiole with its rostral end upward and its caudal end downward, so the other way round, when compared with the other generations. The

acute projections of the caudal stigmata are also stuck into the leaf stalk tissue. The broad room in the petiole in which the pupa occurs is often closed off by a small plug of loosened cells. As already mentioned this third generation has not made a window for emergence.

#### Emergence and hibernation

According to Schütte (1921) the pupal stage of the summer generation lasts 2—3 weeks. At the time of emergence the adult, originating from a pupa of the first or second generation, crawls out of the pupal skin and out of the leaf stalk via the window by means of its ptilinum. The new adult rises towards the water surface because its specific gravity is less than that of water.

The third generation hibernates as pupa and stays in the leaf stalk as long as possible until the petiole tissue has completely decomposed. During the decomposition of the leaf stalk, the pupa together with parts of the petiole, can sink towards the bottom of the pool, but when the petiole has decayed too much the pupa rises to the water surface. The pupal skin is partly filled with gas so that the pupa remains floating. In the Oude Waal floating pupae could not be found in autumn or the first part of the winter. In spring however a few of them were found between material washed ashore. Apparently the decomposition rate of the leaf stalks is not very fast; the pupae can stay a fairly long time in the petioles before they rise to the surface or wash ashore.

During the hibernation period a lot of pupae die; the spring generation is only very small, while in autumn most petioles of *Nuphar* contain pupae of *H. livens*. The solid pupal skin of the winter pupae has probably the function of protection against ice, predators or desiccation.

#### SUMMARY AND DISCUSSION

There are several relationships between the fly *H. livens* and the vegetation dominated by *Nuphar lutea*.

Adult *H. livens* visit the flowers of *Nuphar* for several reasons, viz.:

(a) collecting food in the form of nectar, furthermore preying in the flowers on soft skinned insects or on *Notiphila brunneipes* eggs;

(b) protection and shelter against bad weather conditions, e.g. heavy rain;

(c) resting site; the temperature in the flowers is higher than those of the surroundings during sunny weather conditions (table 3), which

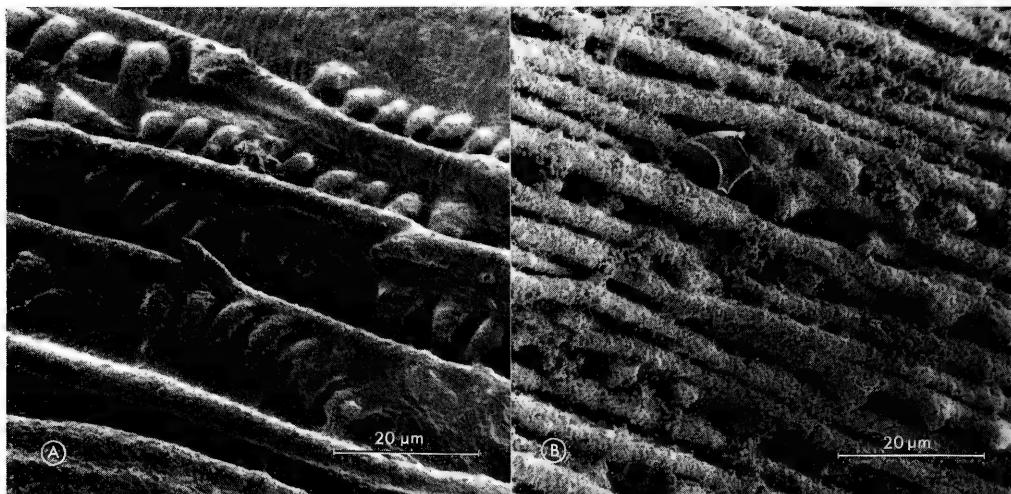


Fig. 25. Scanning electron microscope photographs of the skin of a summer (a) and a winter pupa (b).

probably is favourable for the flies (faster digestion and warming up of flight muscles);

(d) copulation site.

By their regular occurrence in the flowers and by their activities, the flies can cause pollination. In the areas investigated flowering of *Nuphar* took place from mid-June to mid-August so that predominantly the second generation of *H. livenus* could visit *Nuphar* flowers.

Adult *H. livenus* visit the nymphacid floating leaves for:

(a) food; the fly preys here on Chironomidae and *Hydrellia* while the water drops occurring on the floating leaves are used for drinking;

(b) copulation site;

(c) egg deposition; oviposition takes place under the floating leaves of *Nuphar*;

(d) resting site, e.g. for sunning; the upper surface of the floating leaves can reach temperatures higher than those of the ambient air and water (table 3);

(e) shelter against bad weather conditions under aerial leaves of *Nuphar* and *Nymphaea* or leaf margins which have been curled up and dried out.

Because of their many activities on floating leaves, adults of *H. livenus* might function as vectors of spores of parasitic fungi, which occur on the floating leaves such as *Glomerella cingulata* (Ston.) Spauld. et Schrenk. From mid-August till October decomposition of the nymphaeids exceeds production; at this time also the population of adult *H. livenus* is at its maximum.

The eggs are deposited upon the underside of the floating leaf blades. An advantage of this kind of oviposition might be protection against desiccation and against predators such as adults of the own species or parasites.

The larvae and pupae of *H. livenus* are bound to the floating leaves and petioles of *Nuphar*. The leaf blades and petioles function as:

(a) food; the larvae consume mesophyll and petiole tissue, creating mine galleries in this way;

(b) protection; the larvae and pupae are protected against possible predators in these mine galleries;

(c) oxygen supply; the larvae obtain oxygen from the intercellular cavities; the pupae thrust their caudal stigmata into the petiole tissue, obtaining oxygen in this way.

The consumption of living tissue by *H. livenus* larvae initiates a decomposition process in the floating leaves of *Nuphar*. The tissue around the mine galleries very soon decays because of infection by fungi and bacteria. The consumption and damage caused by *H. livenus* in this way can amount to 5—10% of a floating leaf blade (Van der Velde, 1978), when the larval numbers have reached their maximum.

Parts of the leaf blades break off easily by wind and wave action on places where mine tracks of *H. livenus* occur. Also the petioles break off easily on places where the larvae have pupated. In 1977, 15.3% of the floating leaves in the Haarsteegse Wiel and 11.7% of the leaves

Table 8. Comparison of the most important features of the life histories of *H. livens* and *H. confluens*.

	<i>Hydromyza livens</i>	<i>Hydromyza confluens</i>
Food plant(s)	<i>Nuphar lutea</i> (L.) Sm. <i>Nuphar pumila</i> (Timm) DC. <i>Nuphar</i> × <i>intermedia</i> Ledeb. ( <i>Nuphar advena</i> Ait.)	<i>Nuphar advena</i> Ait.
Geographical distribution	Europe and Asia	North America
Number of generations	2—3	2?
Adults		
Food - on leaves - in flowers	Chironomidae, <i>Hydrellia</i> nectar, soft-skinned insects, <i>Notiphila</i> eggs	dead bodies of <i>Chironomus</i> spp. pollen ?, liquid substances
Pollinator	+	+
Spatial occurrence	more abundant on floating leaves bordering the open water	more abundant on floating leaves bordering the open water
Copulation site	flowers and floating leaves	flowers and floating leaves
Oviposition site	underside of leaf-blades of floating leaves	submerged petioles of floating leaves
Deposition of eggs	singly	singly
Air coat when going under water	+	+
Eggs		
Plastron	+ ?	?
Larvae		
Food	leaf- and petiole tissue	petiole tissue
Type of damage	mine gallery	interior excavation of petiole
Construction of window for emergence	+	+
Pupation site	in petiole	in petiole
Pupae		
Occurrence of summer pupae	+	+
Occurrence of winter pupae	+	?

in the Oude Waal separated and floated away, a process in which *H. livens* plays an important role.

These free floating parts of leaf blades and leaf stalks can have an important function elsewhere for other organisms for instance for the hydrozoan *Cordylophora caspia* (Pallas) (Roos, 1979).

From all these data it can be concluded, that the fly *H. livens* is an important element in the nymphaeid ecosystem dominated by *Nuphar*.

It appears from this study on *H. livens* and that of Welch (1914, 1917) on the North-American species *Hydromyza confluens* that the life-histories of both species in many ways resemble each other. The most important features of both *H. livens* and *H. confluens* are summarized in table 8.

Both flies have an important function in nymphaeid vegetation, *H. confluens* in stands dominated by *Nuphar advena* and *H. livens* in similar habitats dominated by European *Nuphar*

taxa. Furthermore, it is interesting that *H. livens* has the ability to affect the natural food plant of *H. confluens*. It is not known whether the larvae of *H. confluens* can also complete their life cycle on European *Nuphar* taxa. It should be mentioned that Beal (1956) considers *Nuphar lutea* (L.) Sm., *Nuphar pumila* (Timm) DC. and *Nuphar advena* Ait. to be subspecies of one species, viz. *Nuphar lutea*. Berg (1950) reports a normal development of a *H. confluens* pupa in the silty, humous bottom of a stream with respirating plates embedded in a root of *Potamogeton alpinus* Balb.

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We are much indebted to Prof. dr. C. den Hartog and to Mr. J. Krikken for critical remarks, to Dr. P. J. van Helsdingen and Dr. W. J. Kabos for the help with the identification of the flies, and to Mr. A. W. Dicke for making the SEM photographs and to the Illustration Service of the University for preparing drawings.

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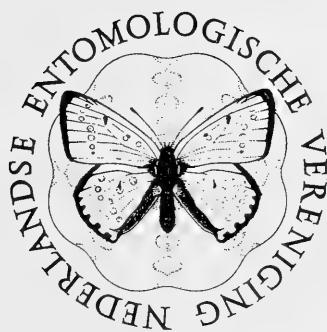




# TIJDSCHRIFT VOOR ENTOMOLOGIE

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## INHOUD

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# COPULATION IN *EPHIPPIGER* (ORTHOPTERA, TETTIGONIOIDEA)

by

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## ABSTRACT

Observations have been made in a number of *Ephippiger* species from Southern France and the role various reproductive structures play during the copulatory process.

## INTRODUCTION

A number of species belonging to the genus *Ephippiger* occur in Southern France and in the adjacent parts of Spain and Italy. In some cases these species vicariate geographically, but there are also several instances of overlapping distribution of two or more species. The question has to be raised whether all taxa distinguished as species (e.g. Chopard, 1951; Harz, 1969) are reproductively isolated. In this paper we will investigate whether the interspecific differences in the form of cerci, epiproct, titillators and subgenital plate could function as mechanical barriers possibly operating against interspecific matings. In another, the next, paper the likelihood of interspecific mating is dealt with.

## MATERIAL AND METHODS

Animals of six species were collected during field trips in August and September, 1977, 1979 and 1980. They were measured and taken to the laboratory where observations were made during the second half of September and during October. In November most animals died. Detailed observations of copulations were made with a stereomicroscope (magnifications 6.5—16×). Some copulations were documented by photography or videorecording.

The species studied and their collecting stations are the following.

*Ephippiger ephippiger* (Fieb., 1784): Niaux (Ariège) 1977, 1979; Mézel (Ht. Provence) 1979, 1980; Causse de Larzac (Aveyron) 1979; Plan d'Aups (Var) 1979, 1980.

*Ephippiger cunii* (Bol., 1877): Mont Louis

(Pyr. Orient.) 1977, 1979; Canigou (Pyr. Orient.) 1979.

*Ephippiger cruciger* (Fieb., 1853): Neffiès (Hérault) 1979; Leucate (Aude) 1979.

*Ephippiger provincialis* (Yers., 1854): Plan d'Aups (Var) 1979, 1980.

*Ephippiger terrestris* (Yers., 1854)<sup>1)</sup>: Mézel and several other places in the vicinity of Digne (Ht. Provence) 1979, 1980, 1981; Fayence (Var) 1980; Col de Braus (Alp. Mar.) 1980; Tende (Alp. Mar.) 1980.

*Ephippiger bormansi* (Br., 1882)<sup>1)</sup>: Col de Tende (Alp. Mar.) 1980; Vallone del Arma (Piemont) 1981.

Some pairs were killed during or just after copulation and preserved to study the position of the genital organs and their elements with respect to each other as well as the position of the spermatophore.

## THE COPULATION

### Description of the behaviour

The general course of copulation in *Ephippiger* er conforms to that in other Tettigonoids, as described by Gerhard (1913, 1914). A short description will be given here emphasizing the details relevant to the questions raised.

A normal copulation will take about half an hour. *Ephippiger* males stridulate during part of the day and night, while sitting on a plant or bush, the height of which generally does not exceed two metres. A sexually motivated female will walk straight to a stridulating male (Busnel & Dumortier, 1954; Duijm & Van Oijen, 1948). On encountering the male the female stops. Both male and female touch each other with the antennae. The male may tremble with his body several times (Busnel et al., 1955). After some time the male will place the extremity of his ab-

<sup>1)</sup> Nadig (1980) considers *E. bormansi* a subspecies of *E. terrestris*, but the conventional classification is retained here for the time being.

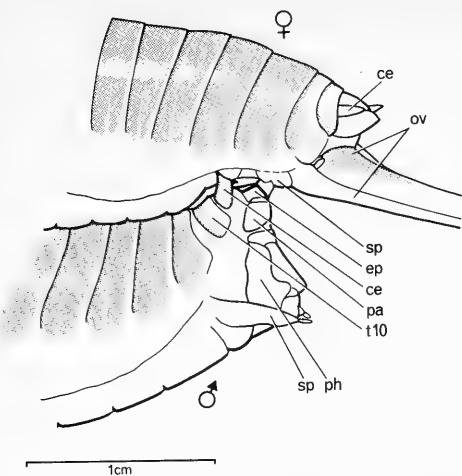


Fig. 1. A pair of *Ephippiger ephippiger* just before the cercal clamp: *ce*, cercus; *ep*, epiproct; *gr*, copulatory groove; *ov*, ovipositor; *pa*, paraproct; *pb*, phallus with: *ll* lateral lobes, *dl*, dorsal lobes and *vl*, ventral lobes; *pl*, pleural region; *sa*, saddle-like part of spermatophore; *sp*, subgenital plate; *st*, stylus; *sx*, spermatophylax; *s6*, sixth sternite; *t9*, ninth tergite; *t10*, tenth tergite.

domen in front of the female's head; the female will then touch the male's somewhat ventrally curved abdomen with her maxillary palps. Moving forward slowly, continually touching, she finally mounts the male's back. When the female has entirely mounted, the male bends his abdomen dorsally, extends the lobes of the phallus and turns his subgenital plate downward. The titillators are now visible between the phallus lobes. The cerci are extended and spread in a laterodorsal direction. The female is now sitting on the back of the male with her head above his pronotum and the median planes of both partners have to coincide at this point. In the female the caudal part of the ventral abdominal wall is contracted, the ovipositor making an angle of 20–45° with its longitudinal axis (fig. 1). Only in this position the female's subgenital plate is situated between the male's cerci in such a way that the copulation may proceed. The male circles with its cerci caudally and medially. Suddenly the inner teeth of the cerci get a grip on the female's subgenital plate and at the same time the cerci clamp the female tightly. Clamping does not occur randomly, but only on two small grooves — the copulatory grooves — which are easy to distinguish by their dark colour, owing to extra sclerotisation. By adducting the cerci the male pulls the female firmly against

its body. In this position the epiproct pushes dorsocaudally against the female's subgenital plate and provides one of the factors for determining the position of the male abdomen with respect to the female's. At the same time, pushing the epiproct against the female subgenital plate results in the lifting of the caudal part of the subgenital plate from the female gonotrema. By this action the gonotrema will be opened up and exposed. Immediately after being clamped, the female brings the ovipositor downward very rapidly to such a position that it fits in the emargination of the caudal rim of the subgenital plate and contacts the styli (fig. 2). After some seconds the ovipositor returns to its normal position. The function of this action is not clear. Perhaps in this way a final check is made to determine whether the partners are in the correct position to enable the next step in the copulation procedure, viz., the rotation. In this position the male will extend and contract the phallus alternately. The female now makes a few steps forward, the male meanwhile somersaulting until he gets hold of the female's ovipositor with his fore and middle legs (fig. 3). In doing so, the male is rotated about an axis through the inner cercal teeth. This rotation is only possible when the cerci are tightly clamped. The position of the male is now entirely fixed with respect to the female and evidently in the only one in which the spermatophore can be deposited. When extended the phallus now reaches the basis of the ovipositor. The phallus makes pulsat-

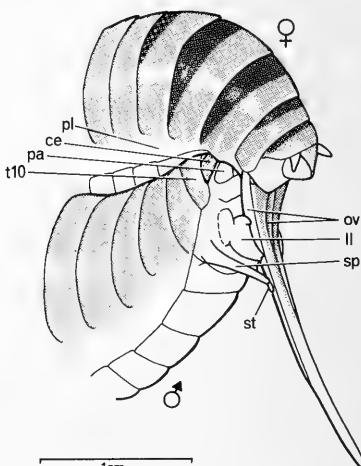


Fig. 2. The position of male and female *E. ephippiger* immediately after the cercal clamp, the female having lowered the ovipositor to contact the male's subgenital plate and styli. See fig. 1 for explanations.

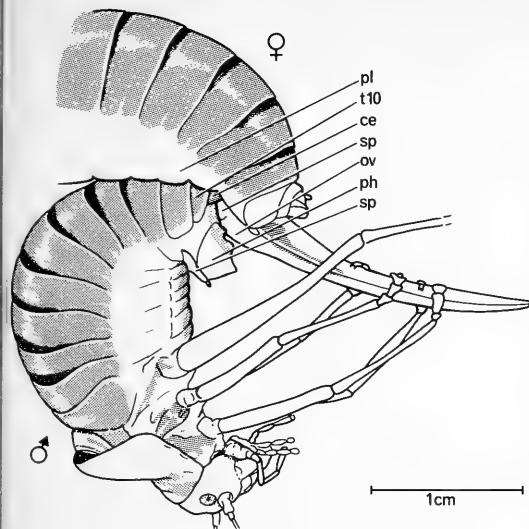


Fig. 3. The relative position of male and female after the rotation in *Ephippiger*. See fig. 1 for explanations.

ing movements during which its dorsal lobes, together with the apical parts of the titillators, will glide over the basis of the ovipositor. After a number of very intensive pulsating movements the apical parts of the titillators will be put into the female's gonotrema at the basis of the ovipositor. Thereafter, the pulsating movements of the phallus will continue for a while but less intensively: meanwhile the titillators in the gonotrema are moved backward and forward. They are dorsocaudally directed and their apices reach the roof of the genital chamber, where the female's genital lobes are situated. Possibly these genital lobes are expanded during this phase. After some time the pulsating movements stop, the phallus being in a maximally extended position. The phallus lobes part and the spermatophore is extruded (fig. 4a). The globular caudal part of the spermatophore bears dorsally a saddle-like structure. With the aid of the phallus the male pushes the spermatophore with the saddle against the ventral valves of the ovipositor (fig. 4b). The saddle is sticky so that the spermatophore adheres to the ovipositor for some time.

The phallus is then contracted, especially its dorsal lobes (fig. 4c). In this phase the stalk of the spermatophore is inserted into the gonotrema. At the same time the female will make sculling movements with the ovipositor by moving the right and left valves with respect to each other rostrally and caudally, respectively.

Apparently the female is playing an active role while receiving the spermatophore. At the end of this phase the extremity of the stalk of the spermatophore is firmly held by the genital lobes in the genital chamber.

After some seconds follows the deposition of the spermatophylax, a rather voluminous gelatinous mass (fig. 4d). Meanwhile the male withdraws the phallus from the spermatophore. The titillators have been withdrawn from the gonotrema and are visible again. The female will now make some strides, the cerci will loosen and the partners part. The male's phallus is contracted and the subgenital plate closed. The female will soon begin to eat parts of the spermatophylax and ultimately, after an hour or so, also the spermatophore. In the meantime sperm from the spermatophore has had ample opportunity to enter the female's spermatheca. The openings of the sperm canals in the spermatophore-stalk are situated just opposite the entrance to the spermatheca.

### Experiments

The role of the inner cercal teeth was verified by carefully cutting them away. This was done in males of *E. ephippiger* and *E. terrestris*. Five copulation attempts by these experimental males were observed, all showing the same course. After mounting, the female performed downward movements with the ovipositor without however reaching the male's subgenital plate. Although the male tried to grasp the female with his cerci, he never succeeded. It is concluded that the inner cercal teeth are essential for providing a hold on the female. Furthermore, these experiments showed that the fully deflected position of the ovipositor will only be realised as a reaction to the accomplishment of the cercal clamp.

With regard to the role of the titillators the following morphological information is relevant. A male has two symmetrical titillators. Each titillator consists of a basal part, on which two muscles insert, and an apical part, which may protrude from the phallus lobes. The latter enters the female gonotrema during copulation. One muscle inserts on the lateral part of the titillator basis and originates from the apodeme of the 10th tergite. This muscle is probably homologous with the ventral retractor muscle (Snodgrass, 1940). The other muscle inserts on the medial part of the titillator basis and has its origin on the subgenital plate. This muscle is the homologue of Snodgrass's dorsal retractor mus-

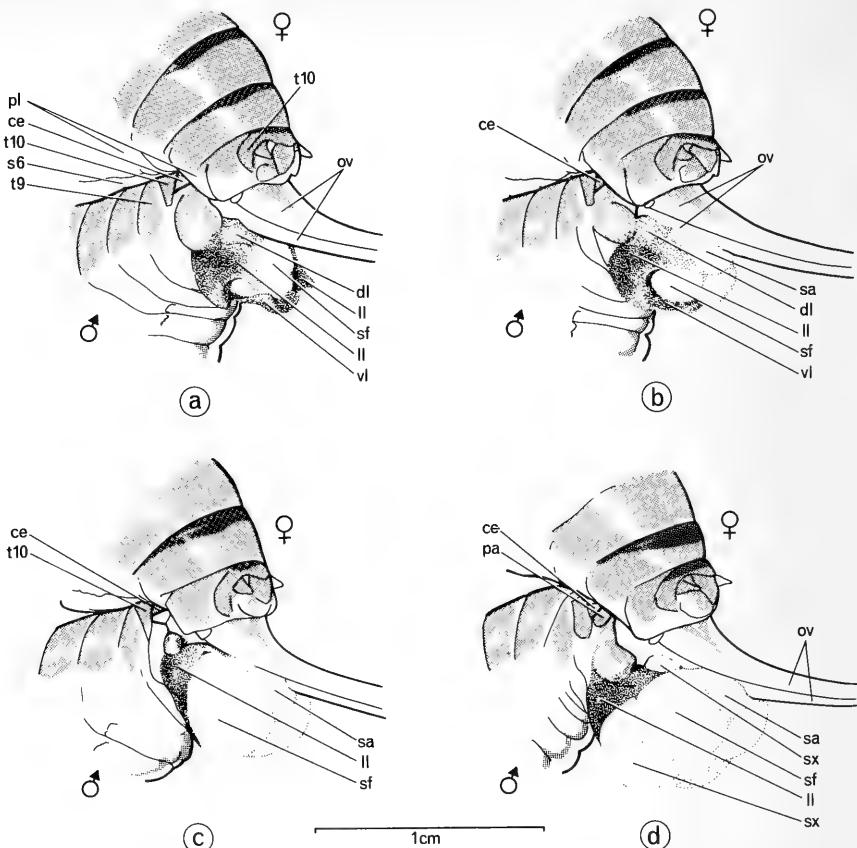


Fig. 4. Production of the spermatophore in *Ephippiger*: (a) the globular part of the spermatophore becomes visible; (b) the saddle-like part of the spermatophore is being pressed against the ovipositor; (c) the dorsal lobes of the phallus are being contracted; (d) the spermatophylax appears. See fig. 1 for explanations.

cle. The following movements have been observed: (a) dorsal deflection, (b) lateral deflection. In (a) and (b) the apices of both titillators stay close together pointing in the same direction, whereas when the phallic lobes are maximally extended, the apices may diverge. To obtain some insight into the way the titillators function during copulation the following experiments were performed. In eight males of *E. ephippiger* the apical parts of the titillators were cut off. Both titillators were shortened to the same extent, but the length of the cut parts differed. In the extreme case the entire denticulated part was removed. The operation did not alter sexual motivation or copulatory behaviour. One copulation was observed in each male. In no case were the remnants of the titillators inserted into the female's gonotremma, inde-

pendent of the length of the remaining part. Probably the cut ends of the titillators cannot readily enter the gonotremma because they lack the rounded apex which is characteristic of the intact titillator. Notwithstanding the lack of insertion, a spermatophore was deposited in all cases. In half of these cases the stalk was brought into the normal position within the gonotremal space. In the remaining cases this did not occur and the female then lost the spermatophore immediately after the copulation. From these observations it follows that the insertion of the titillators is not a prerequisite for completion of the copulation. Evidently the action of the male's phallic lobes together with the action of the female's genital lobes may result in normal reception of the spermatophore stalk. The number of failures was nevertheless high;

this points to the role of the titillators in providing additional reliability. In our opinion the titillators do not play a role in opening up the female gonotrema nor in delivering a stimulus to the female, which is essential for receiving the spermatophore. Insertion of the titillators into the gonotrema probably orientates the position of the gonotrema just opposite the male's gonophore. In the end phase of copulation, the titillators are situated against the rostral wall of the gonotrema in such a way that the stalk of the spermatophore may glide along the smooth ventral sides of the titillators and in this way may be led to the gonotrema, as by a shoe-horn. Because the curved denticles on the apical parts of the titillators are situated on their dorsolateral sides, they will therefore grip the rostral wall of the gonotrema in the end phase of the copulation. Without this gripping, however, successful insertion of the spermatophore still remains possible. In two other males of *E. ephippiger* a part of only one titillator was cut off, the other being left intact. Insertion appeared to be normal in these males during copulation. In one copulation the stalk of the spermatophore was inserted quite normally, in the other case the spermatophore was lost by the female. In the latter case, orientation of the male gonopore with respect to the female's gonotrema was in our view not precise enough to ensure reception of the stalk by the female's genital lobes.

#### DISCUSSION

The copulatory behaviour in *Ephippiger* consists of two closely interlocked complementary series of movements by male and female. Both female and male copulatory apparatuses function as mechanical systems of considerable complexity. For their successful interaction not only has highly standardised behaviour to be performed, but also the form and dimensions of the various parts in male and female must conform to a high extent. In the course of the copulation a consecutive series of mechanical conditions has to be satisfied after the female has mounted:

- (1) do the median planes of both partners coincide?
- (2) is the female's subgenital plate situated between the male's cerci?
- (3) can the inner cercal teeth get a hold in the copulatory grooves of the female's subgenital plate?
- (4) does the ventrally deflected ovipositor fit the emarginated rim of the male's subgenital

plate so that their gonopores are just in front of each other?

- (5) do the phallic lobes with the titillators reach the female's gonotrema?

Only when all conditions are fulfilled is the cercal clamp carried out correctly and rotation ensues. After this, spermatophore and spermatophylax will be produced and the spermatophore stalk will be inserted into the female's gonotrema when:

- (6) the titillators have been introduced in the gonotrema.

Form, position and size of the various parts of the genital apparatus have to correspond; it is analogous to a lock and key system. However, this system does not appear to be very rigorously determined: interspecific copulations may occur occasionally under laboratory conditions. Moreover, not every morphological detail appears to be of decisive importance as is indicated by the experiments with cut titillators.

In the following paper, the differences between species with regard to their genital apparatus and copulatory behaviour will be considered together with the possibility of interspecific matings.

#### SUMMARY

The course of copulation in the genus *Ephippiger* has been described emphasising the succession of mechanical conditions that must be satisfied for the copulation to be completed. The male cerci play a central role; they have to grasp into the copulatory grooves on the female's subgenital plate with their inner teeth. Only after having successfully clamped the female does the male rotate about the axis through the inner cercal teeth and continues copulation. The titillators appear to be used as shoe-horns for guiding the spermatophore stalk when it is being introduced into the female gonotrema.

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# INTERSPECIFIC MATING IN *EPHIPPIGER* (ORTHOPTERA, TETTIGONIOIDEA)

by

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## ABSTRACT

A number of (sub)species of *Ephippiger* were compared with respect to the possibility of interspecific mating, differences in the morphology of genital parts and geographical distribution. A tentative conclusion on the taxonomic status of the (sub)species studied is presented.

## INTRODUCTION

In Southern France a number of species of the genus *Ephippiger* occur, which are mainly endemic. Their morphological characters are rather variable and show extensive overlapping. Therefore, the question may be raised whether this situation is at least partly due to interspecific interbreeding. Nadig (1980) postulates an extensive hybridisation zone in the French Alps between *Ephippiger terrestris* and *E. bormansi*, which he considers subspecies. To look further into this matter we have, in the preceding paper (Duijm, Oudman & Veldstra, 1983), analysed the copulatory behaviour in *Ephippiger* in general, emphasising those morphological and positional details that could be decisive in determining whether successful copulation between two partners will be possible. In this paper data are given with regard to the possibility of the occurrence of interspecific matings under laboratory conditions. Moreover, relations between these observations and the morphological differences in the copulatory apparatus are given.

## MATERIAL AND METHODS

Specimens of eight (sub)species of *Ephippiger* were collected during field trips in August and September, 1977, 1979, 1980 and 1981. They were measured and taken to the laboratory where observations were made during the second half of September and October. Animals were kept individually in small cages and fed a diversity of wild plants (e.g. *Stellaria media*

(L.), *Calystegia sepium* (L.), *Aegopodium podagraria* (L.), *Taraxacum* spec.) and occasionally a meal-worm. The cages were regularly sprayed with water and females could deposit their eggs in small boxes with moist turf.

For observation a male and a female were placed together on a branch. During the copulations details were observed with a stereomicroscope (magnification 6.5—16 $\times$ ). Some copulations were documented by photography or by videorecording. The species studied and their collection stations are: (France, unless stated otherwise)

*Ephippiger ephippiger vitium* Serv., 1931: Causse de Larzac (Aveyron), 1979; Niaux (Ariège) 1977, 1979; Mézel (Ht. Provence) 1979, 1980; Plan d'Aups (Var) 1979, 1980;

*Ephippiger ephippiger vicheti* Harz, 1966: Miglieglia (Ticino, Switzerl.) 1980, 1981; Naggio (Lago di Como, Italy) 1981;

*Ephippiger cunii* Bol., 1877: Mont Louis (Pyr. Orient.) 1977, 1979; Canigou (Pyr. Orient.) 1979;

*Ephippiger cruciger* (Fieber, 1853): Neffiès (Hérault) 1979; Leucate (Aude) 1979;

*Ephippiger provincialis* (Yers., 1854): Plan d'Aups (Var) 1979, 1980, 1981;

*Ephippiger terrestris* (Yers., 1854)<sup>1)</sup>: Mézel and several other places in the vicinity of Digne (Ht. Provence) 1979, 1980; Collobrières (Var) 1980; Fayence (Var), 1980; Col de Braus (Alp. Mar.) 1980; Gréolières (Alp. Mar.) 1981; Col de Brouis (Alp. Mar.) 1981; Col de Castillon (Alp. Mar.) 1981; Tende (Alp. Mar.) 1980; Cle. Scraïvaon and Mt. Carmo (Ligur. Alps, Italy 1981;

*Ephippiger bormansi* (Br. v. W., 1882)<sup>1)</sup>: Col de Tende (Alp. Mar.) 1980, 1981; Vallone del Arma (Piemont, Italy) 1981; Naggio (Lago di

<sup>1)</sup> Nadig (1980) regards *E. bormansi* as a subspecies of *E. terrestris*; the conventional classification is retained here for the time being.

Como, Italy) 1981; Miglieglia Ticino, Switzerl.) 1981.

#### THE RESULTS OF ATTEMPTS TO INTERBREED IN THE LABORATORY

We shall confine our attention to successful copulations. In this paper we speak of a successful copulation when the copulatory process takes the normal course and the spermatophore stalk is correctly inserted into the female's gonotrema. No observations were made on subsequent fertilisation nor on the development of the eggs. The crosses attempted are dealt with below.

##### (1) *Ephippiger ephippiger*

Not all pairs of *E. ephippiger* formed by bringing together males and females of different populations copulated successfully. In all three cases observed of crossing a female of the subspecies *E. e. vicheti* with a male of the subspecies *E. e. vitium* (from different sources) the male's attempt to clasp the female failed; apparently the male's abdomen was too broad and therefore the distance between the cerci too big for getting hold in the female's copulatory grooves. No data are available at the moment on the reverse combination (*E. e. vicheti* ♂ × *E. e. vitium* ♀).

Among the populations studied of the subspecies *E. e. vitium* there is one that differs considerably from the others. This is the population from Niaux, where the animals are rather big. Their titillators are shorter than in the other populations of *E. e. vitium* and as seen in lateral view, they are more curved. Moreover the apical part, bearing teeth, is longer. There are also differences in song. Because of this heterogeneity the observations with specimens of *E. e. vicheti* and *E. e. vitium* from Niaux are left out of consideration when dealing with crosses between *E. ephippiger* and other *Ephippiger* species.

##### (2) *Ephippiger terrestris*

Ten copulations were observed between twenty individuals from different sources. In all cases copulations were performed, notwithstanding the different sources and body sizes. The samples included rather small animals (forma *minor*, collected 1200 m above sea level) and rather big animals (nominate form, collected at 300 m), the difference in body length amounting to 15–25%. Also specimens from Tende, probably belonging to the subspecies *E. terrestris caprai* Nadig (1980) were included. Later observations showed the possibility of

successful copulations between *E. terrestris terrestris* and *E. terrestris caprai* (from Cle. Scraavon and Mt. Carmo in the Ligurian Alps).

##### (3) *Ephippiger bormansi*

One copulation between a pair of *Ephippiger bormansi* (from Col de Tende) was observed. As was expected the copulation ended successfully.

##### (4) Crosses between *E. terrestris* and *E. bormansi*

On three occasions an *E. terrestris* ♀ was placed together with an *E. bormansi* ♂ (from Col de Tende). In all cases copulation was successful. The same applies to the reverse combination: four successful copulations were observed. Later on, successful copulations were observed between *E. bormansi* (from Vallone del Arma and from Naggio) with *E. terrestris caprai* (both from Tende and from Mt. Carmo) and with *E. terrestris terrestris*.

##### (5) Crosses between *E. terrestris* and other *Ephippiger* species (excluding *E. bormansi*)

Six females of *E. terrestris* were placed with an *E. ephippiger vitium* male and two females of *E. terrestris* with a male of *E. cunii*. In none of these cases did a successful copulation ensue. Generally the female mounted and brought the ovipositor downward. The male tried to clamp the female with his cerci but did not succeed in getting hold on the female's subgenital plate. The same result was obtained when placing a female *E. bormansi* with an *E. ephippiger* male.

On two occasions an *E. terrestris* male was placed with an *E. ephippiger* female. In both the male clamped the female with the cerci, but on the wrong place, i.e. on the soft rostral parts of the seventh sternum and not on the sclerotised copulatory grooves. In one of these cases the male pierced the female sternal wall whereupon the female left the male. In the other case, the copulatory rotation was effected and the male extruded the phallus. During pulsating movements of the phallus the titillators glided over the open gonotrema but they were not inserted. A spermatophore was deposited but was lost by the female immediately after the copulation; obviously the spermatophore stalk had not been inserted into the female's gonotrema. This failure was probably due firstly to the male gonopore not being placed precisely opposite the female's gonotrema and secondly to the titillators not being able to conduct the spermatophore stalk.

Comparable results were obtained in combinations (two cases) consisting of a male *E. bor-*

*mansi* and a female *E. ephippiger*.

(6) Crosses between *E. ephippiger* and *E. cunii*

As might be expected successful copulations between *E. cunii* males and females were readily obtained.

On three occasions a male *E. cunii* was confronted with a female *E. ephippiger*: in one case the cercal clamp did not succeed; in the second case the cercal clamp held only for a short time; in the third case the cercal clamp held only after five failures. In the latter rotation followed and the titillators were inserted. After that the copulation attempt was terminated because the female fled.

On two occasions a male *E. ephippiger* was placed with a female *E. cunii*. Neither male succeeded in getting a hold on the female's copulatory grooves and copulation attempts were terminated.

(7) Crosses between *E. ephippiger* and *E. cruciger*

One observation is available on a pairing between a male *E. cruciger* with a female *E. ephippiger*. The male did not succeed in clasping the female definitively; several times the cercal teeth entered the copulatory grooves but time and again they sprang loose with a conspicuous click. The female's abdomen appeared to be too narrow for the male. Similar results were obtained in two comparable cases with female *E. ephippiger* from Niaux. No data are available on the reverse combination owing to a lack of *E. cruciger* females.

(8) Crossings between *E. cruciger* and *E. cunii*.

We have one observation of a fully successful copulation between a male *E. cunii* and a female *E. cruciger*.

#### INTERSPECIFIC DIFFERENCES IN THE MORPHOLOGY OF THE COPULATORY APPARATUS

In order to elucidate the factors that may prevent successful copulation between a variety of *Ephippiger* species, a study was made of morphological characters of those genital parts, that could be relevant to the question raised.

(i) The cerci (fig. 1)

Notwithstanding the rather great variation in cercal form three groups of species may be distinguished with regard to the general form of the cerci and the positioning of their inner teeth, i.e.:

(1) *Ephippiger provincialis*: cercus short and stout with strongly curved inner tooth and also

a strongly curved terminal tooth;

(2) *Ephippiger terrestris* and *E. bormansi* with cerci that are more or less cylindrical in general outline, not conical as in the next group (Nadig, 1960). There is no terminal tooth. The inner cercal teeth are situated just near the cercal apex; in the living animal these teeth lay well behind the hind rim of the epiproct (Nadig, 1960). In preserved specimens this relative position may be altered;

(3) *Ephippiger ephippiger*, *E. cruciger* and *E. cunii*: the cerci are more conical than cylindrical. The inner teeth are not situated near the cercal apex but half or three quarters way along the cercus. In the living male the inner teeth are situated adjacent to the sides of the epiproct.

(ii) The epiproct (fig. 1)

In group 3 the epiproct is entirely sclerotised; the connection with the 10th tergite, however, is not sclerotised and therefore the epiproct is movable with regard to the 10th tergite. On the other hand in group 2 the epiproct itself is not entirely sclerotised: neither its caudal edges nor its lateral rims are hardened. The sclerotised part of the epiproct is, in these species, not movable with respect to the 10th tergite.

(iii) The titillators (fig. 2)

In group 2 the apical parts of the titillators bear one row of denticles, whereas in group 3 there are often more rows of denticles. The basal edge of the titillators is broadened in group 2, but not so in group 3. Seen from the side the apical parts of the titillators are distinctly curved in group 3 and rather straight in group 2. In group 1 the basal parts are strongly upcurved with a broadened end part.

(iv) The seventh sternite and subgenital plate in the female (figs. 3 and 4)

In group 1 nearly the entire subgenital plate is sclerotised, but in group 2 and 3 the seventh sternite and the subgenital plate of the female are only partially sclerotised. The two groups differ clearly with regard to the form of the sclerotised parts. Indications of such differences are present in the systematic descriptions (e.g. Harz, 1969). A more detailed description is given here.

In group 3 the subgenital plate is not as extensively sclerotised as in group 2. The caudal rim is sclerotised and generally there are two separate shield-like sclerotised parts on either side of the midline. (These shields are lacking in *E. ephippiger vichei*). Moreover, the rostral-lateral parts bearing the copulatory grooves are sclerotised. These copulatory grooves are not situated

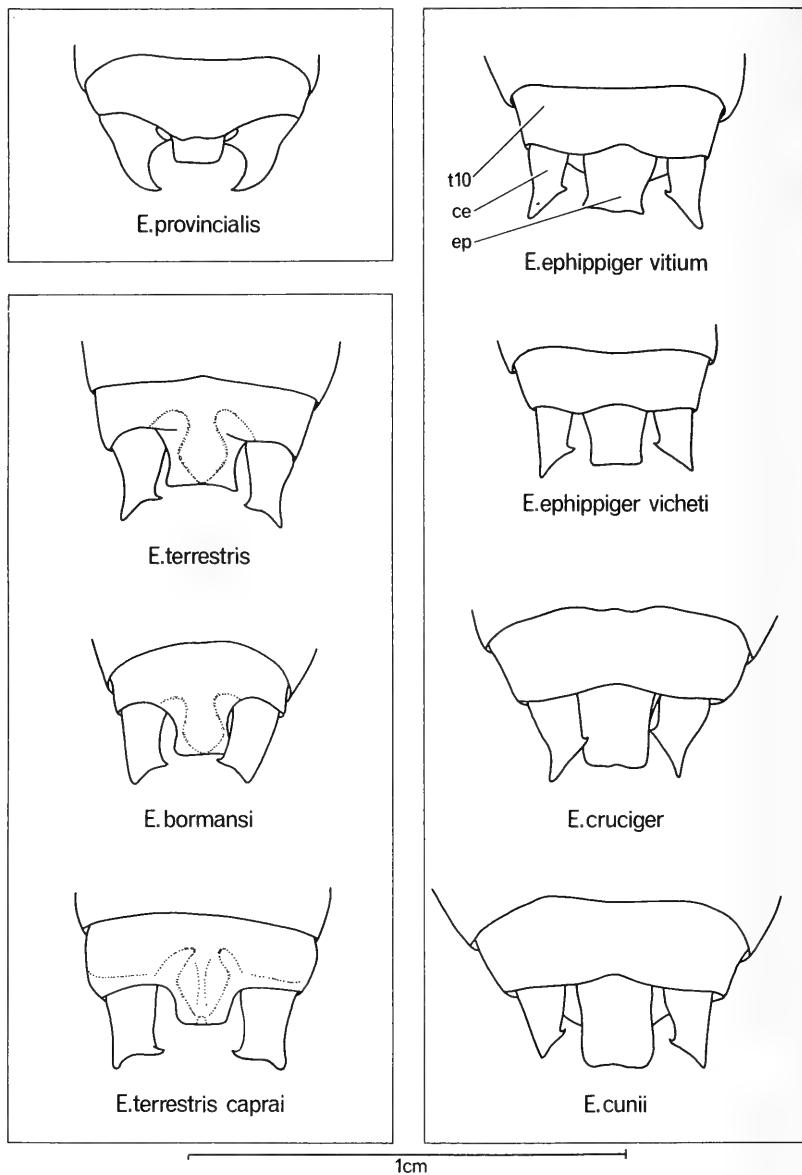


Fig. 1. Hind parts of *Ephippiger* males, dorsal aspect: *ce*, cercus, *ep*, epiproct, *gr*, copulatory groove, *ov*, ovipositor, *pa*, paraproct, *pb*, phallus with: *ll*, lateral lobes, *dl*, dorsal lobes and *vl*, ventral lobes; *pl*, pleural region, *sa*, saddle-like part of spermatophore, *sf*, spermatophore, *sp*, subgenital plate, *st*, stylus, *sx*, spermatophylax, *s6*, sixth sternite, *s7*, seventh sternite, *t9*, ninth tergite, *t10*, tenth tergite.

in an extreme lateral position as in group 2, but more medially. The lateral limit of a groove is rather gradual, but the medial rim is very steep, owing to a very distinct ridge, that is strongly sclerotised.

Owing to the difference in position there is a

significant difference in the distance between the copulatory grooves in group 2 and group 3. On the average, this distance amounts to 10 to 11% of the body length (range 9—12%) in group 3 and 14 to 16% (range 13—17%) in group 2.

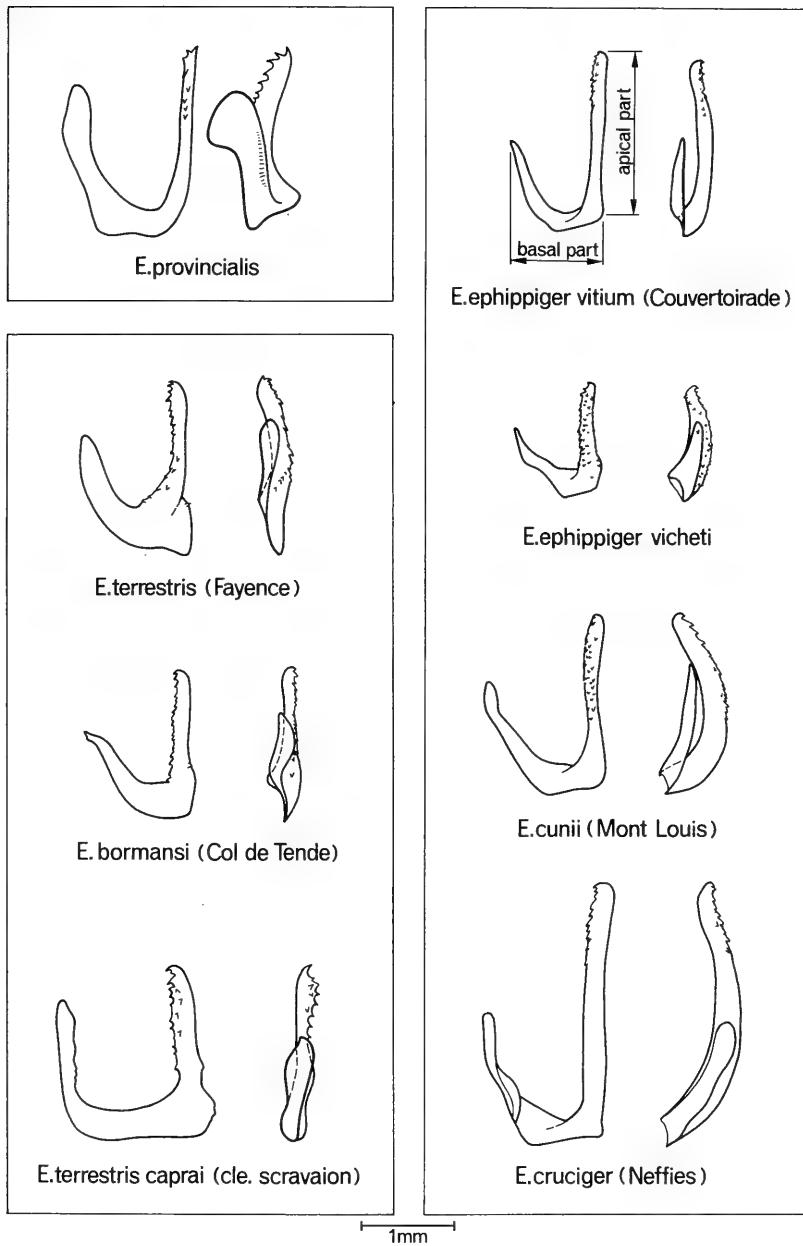


Fig. 2. Right titillators, dorsal view (left), right view (right).

#### INTERSPECIFIC DIFFERENCES IN BEHAVIOUR

##### (i) Trembling

The trembling behaviour in *Ephippiger* is described by Busnel et al. (1955). The animal makes rapid up and down movements with the body, by flexing and extending the legs alterna-

tely while keeping the tarsi to the substrate. The male often trembles after having contact with a female; also the female may tremble in the neighbourhood of a male, but this is seen less frequently. Males may tremble also towards other males. Trembling has been observed regu-

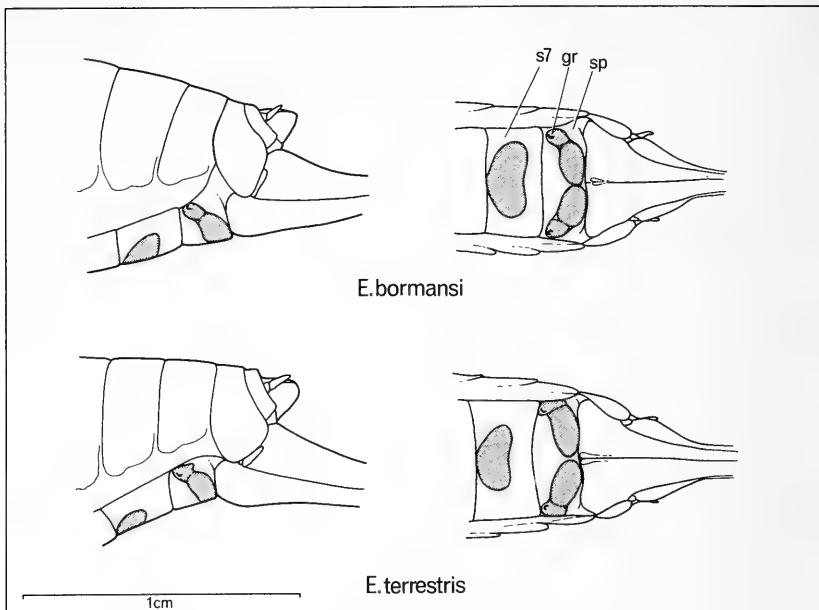


Fig. 3. Hind parts of *Ephippiger* females, group 2, left view (left), ventral view (right); see fig. 1 for explanations.

larly in *E. ephippiger* and also in *Ephippiger cunii*, *E. cruciger* and *E. provincialis*. It has never been observed during copulation preliminaries in *E. bormansi* or in *E. terrestris*.

#### (ii) The course of the copulation

A general description of the course of copulation in *Ephippiger* is given in the previous paper (Duijm, Oudman & Veldstra, 1983). In this paper we restrict ourselves to pointing to an obvious difference in the course of copulation between group 2 and group 3.

Before the cerci clasp the female's subgenital plate, the partners have to position themselves very accurately with respect to each other. The female contracts the caudal part of the sternal wall and directs the ovipositor downward together with the subgenital plate. In this position the male epiproct is directed caudally against the female's subgenital plate. The female's ventral wall (including the medial parts of the 6th and 7th sternum and the rostral part of the subgenital plate) is pushed tightly against the male's tergum including the dorsal side of the epiproct.

In group 3, the caudal rim of the epiproct is held in place by the rostral part of the subgenital plate, but in group 2 by the caudal part of the subgenital plate, which is that part behind the two shield-like sclerotised parts. In both cases

the distance between the copulatory grooves is determined by the connecting sclerotised parts, which are formed mainly by the 7th sternum in group 3 but by the subgenital plate in group 2 (fig. 5).

#### THE GEOGRAPHICAL DISTRIBUTION OF THE EPHPPIGER SPECIES

To judge the likelihood of interspecific matings occurring in the field and to consider the taxonomic status of the taxa dealt with, data on their geographical distributions are essential. Not all data from the literature are usable on account of the confusion often met with regarding the exact distinction between the species. Our interpretation of the pattern of distribution is given in fig. 6 for the (sub)species studied. For the distribution of *E. terrestris* and *E. bormansi* we have mainly followed Nadig (1980) with the addition of a few of our own data. For the distribution of *E. ephippiger* we used the data from Chopard (1951), Harz (1969), Dreux (1962) and Voisin (1979), with some additions and modifications based on our own observations. The distribution of *E. cruciger* and *E. cunii* is mainly based on Chopard (1951) and Busnel (1963), with some additions, as is the distribution of *E. provincialis*.

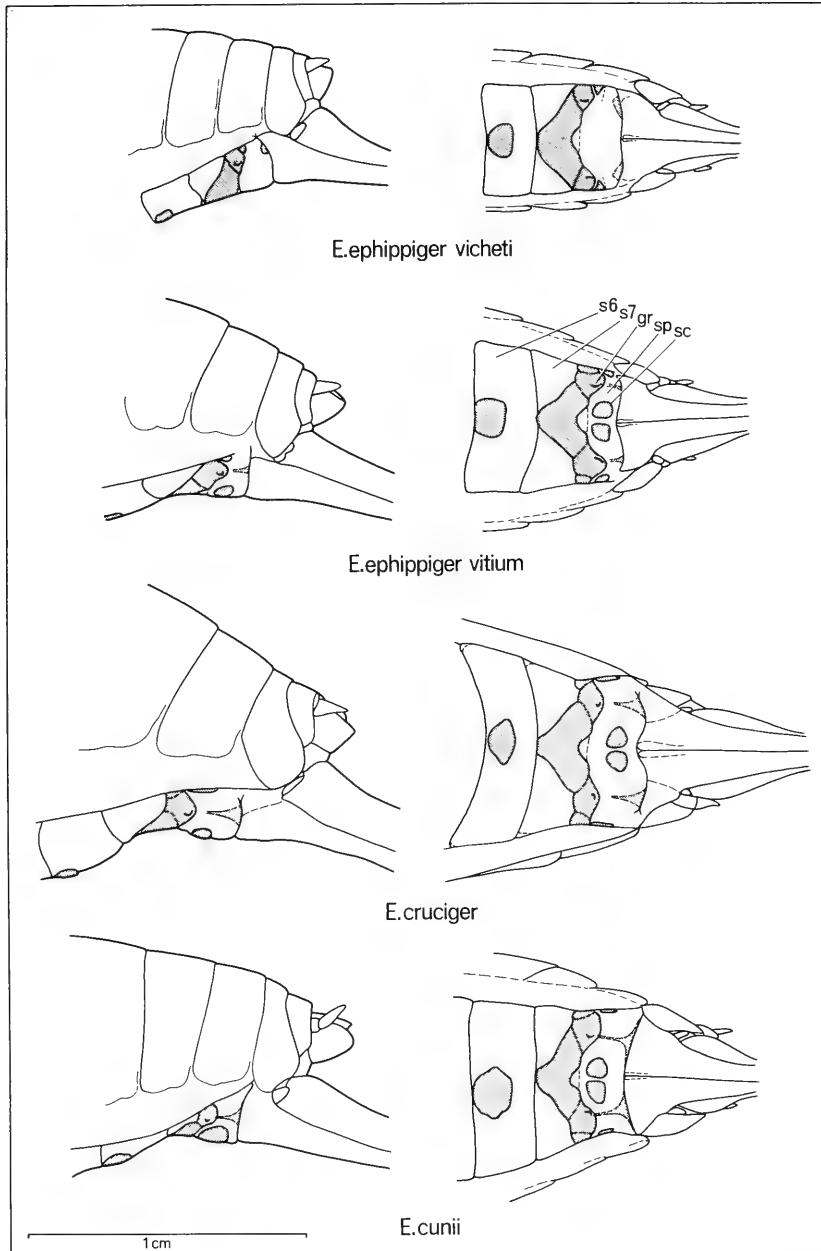


Fig. 4. Hind parts of *Ephippiger* females, group 3, left view (left), ventral view (right); see fig. 1 for explanations.

The first question that comes up now is whether there are species with overlapping areas and if so, whether members of two or more species will indeed meet each other or, at

least, are likely to meet each other in such a situation that interspecific matings could occur. For both of these field investigations are necessary.

From the distributional data available at the

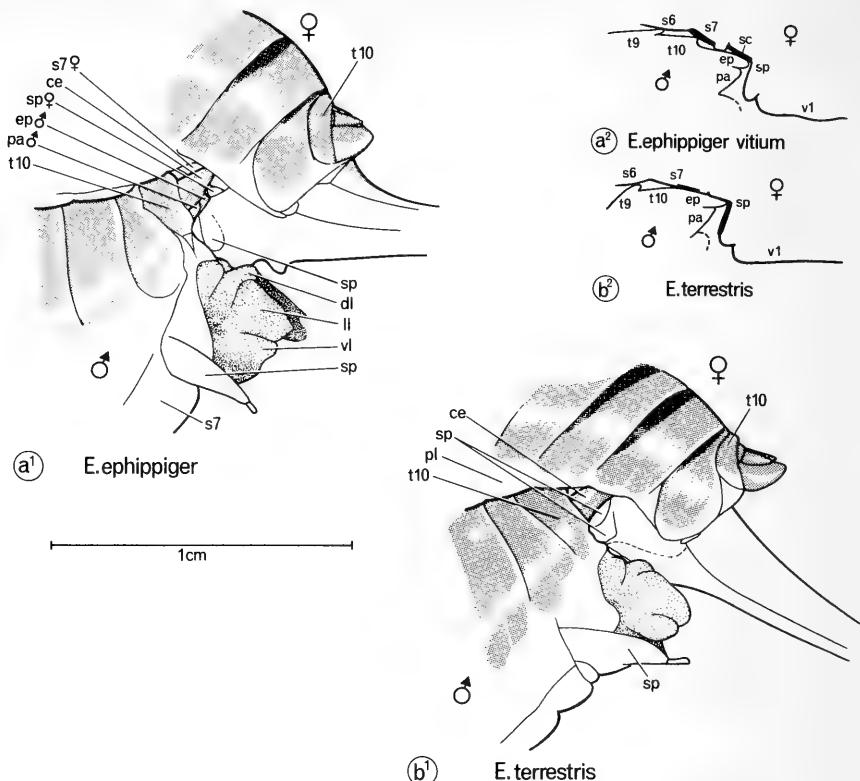


Fig. 5. Comparison of the relative position of male and female *Ephippiger* after cercal clamping; a: *E. ephippiger vitium*, b: *E. terrestris*; a<sup>1</sup>, b<sup>1</sup>: left view; a<sup>2</sup>, b<sup>2</sup>: tentative diagrammatical median section. See fig. 1 for key explanations, sc, shield-like sclerotised area on the subgenital plate in *E. ephippiger vitium*. Highly sclerotised parts in the female indicated by thick lines.

moment it appears that there are only two entirely vicarious species<sup>1)</sup> that vicariate not only mutually, but also with respect to all other species: *E. cruciger* (Chopard's record of its occurrence in Cavalaire (Var) is discarded) and *E. cunii*. Nevertheless, before the existence of contact or overlap zones may be completely precluded, further field investigations are necessary.

*E. ephippiger vitium* and *E. ephippiger vicheti* are considered to vicariate and *E. ephippiger vitium* appears to vicariate with both *E. cruciger* and *E. cunii*.

On the other hand overlapping areas are present between:

(a) *E. ephippiger vicheti* and *E. bormansi*:

<sup>1)</sup> According to Dr. G. Kruseman (pers. comm.), Chopard's (1951) record of *E. perforatus* for France is in error.

Italian-Swiss lake district;

(b) *E. ephippiger vitium* and *E. provincialis*: Plan d'Aups;

(c) *E. ephippiger vitium* and *E. terrestris*: neighbourhood of Mézel and Digne, Gorges du Verdon;

(d) *E. terrestris* and *E. provincialis*: Collobrières;

(e) *E. terrestris* and *E. bormansi*: Col de Tende and, according to Nadig (1980), in a rather broad hybridisation zone in the south-eastern part of the French Alps; possibly *E. terrestris caprai* is also involved.

These cases of overlapping distribution are dealt with below in more detail.

ad (a). According to Nadig's extensive investigations (1968) *E. ephippiger vicheti*, in the northern part of its area (Swiss), lives both at lower and higher altitudes up to 1650 m above sea level. In the southern part (Swiss-Italian lake

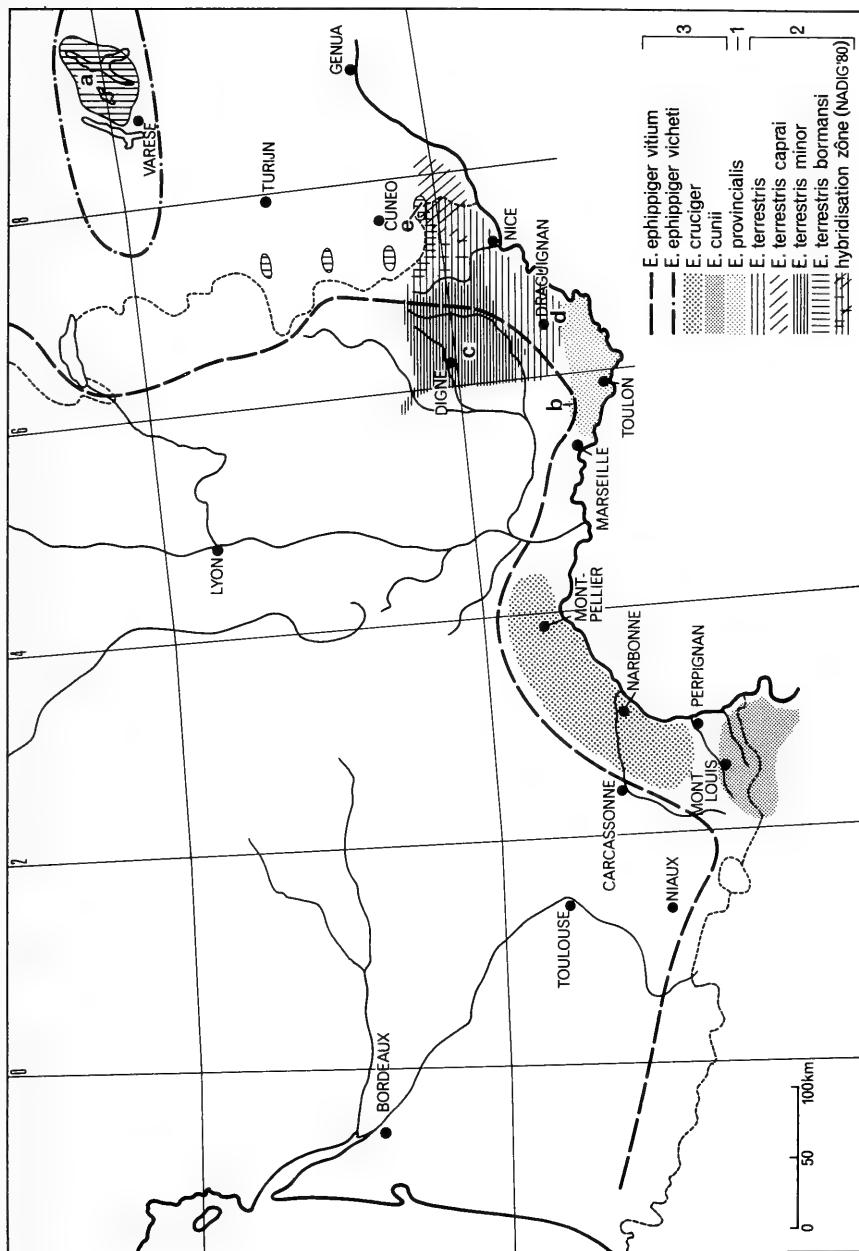


Fig. 6. Provisional map showing the geographical distribution of the *Ephippiger* (sub)species dealt with, following Nadig's (1980) nomenclature.

district), however, where *E. bormansi* also occurs, a distinct niche separation is present, *E. bormansi* occurring above about 1000 up to 1900 m and *E. e. vicheti* occurring at lower altitude. Nevertheless, according to Nadig (1968) both species may live in an intermediate zone (950—1100 m). In September 1981 we found these two species living together above Naggio (Lago di Como) at 750 m and at the foot of the Mt. Lema between 920 and 1100 m. The two species differ considerably in song character and in behaviour. According to our observations in this region *E. e. vicheti* lives much less on exposed shrubs, but more in sheltered places and generally rather high up in trees and bushes, whereas *E. bormansi* occurs more in the open and on lower plants and shrubs. The differences in song will be dealt with in a separate paper. Specimens of both species may meet each other, but there is no indication of hybridisation in the field. This agrees with the laboratory observations reported above (p.o.).

ad (b). In the neighbourhood of Plan d'Aups and Mazaugues (Var) *E. provincialis* and *E. ephippiger vitium* do occur together not only in the same geographical area, but also, to a certain extent, in the same habitat. In the field we had the impression that there is some difference in microhabitat. *E. provincialis* lives preferably on dwarf-shrubs, not more than 50 cm above the ground, whereas *E. ephippiger* mainly lives in the higher parts of bushes and trees, with preference on oaks, blackberry, etc. As might be expected from the considerable morphological differences between these species no hybridisation occurs.

ad (c). As is indicated by Dreux (1962) *E. ephippiger* occurs in the French Alps generally at lower altitudes up to 1500 m (maximally 2000 m). We found *E. terrestris* and *E. ephippiger* occurring together at several places in the Alpes-de-Haute-Provence. In the neighbourhood of Mézel and Digne *E. ephippiger* occurred up to 1100 m and *E. terrestris* from 800 m upwards. In this area *E. ephippiger* lived mainly on bushes and high plants, whereas *E. terrestris* lived chiefly on low herbs and in the meadows.

On the slope leading to the Gol de la Cine (coming from Digne), *E. ephippiger* was found at 770 m and *E. terrestris* at 870 m. In this case no real contact zone could be established.

Near the Gorges du Verdon both species were found occurring in close proximity at 750 m as well as at an altitude of 850 m. In this case, too, *E. ephippiger* showed at preference for

blackberry bushes along the road, unlike *E. terrestris*.

No indication of possible hybridisation was encountered in the field, which is in accordance with the results of the laboratory observations.

ad (d). Near Collobrières (Var) at an altitude of about 130 m, *E. terrestris* lived on bushes, vine and low herbs, whereas *E. provincialis* was found preferentially in vineyards.

ad (e). In the neighbourhood of Tende *E. terrestris* occurs rather commonly at altitudes between 700 and 1000 m. This population belongs probably to the subspecies *E. terrestris caprai* (Nadig, 1980). When climbing to the Col de Tende, we found *E. bormansi* between 1200 and 1750 m, but at lower altitudes individuals were found with intermediate morphological characters (especially with respect to the form of cercus and epiproct). Therefore, hybridisation is likely to occur in this zone.

## DISCUSSION

The six species of *Ephippiger* studied have been arranged in three groups according to the morphology of the cerci and other genital parts. Also described is a difference between group 2 and group 3 in the copulatory positions, that results from these morphological differences. Moreover, the premating "trembling" behaviour has not been observed in group 2.

The data presented above on the occurrence of successful interspecific copulations under laboratory (no choice) conditions agree with the division into three groups: between these groups mechanical barriers to interbreeding prevail, whereas within the groups interbreeding is not excluded in a number of combinations.

Tentative inferences with regard to the grade of relationship may be drawn from the above.

*Ephippiger provincialis* (group 1) forms the only example among the species studied, of completed speciation. In this regard it is interesting that this species is distributed on a very limited area without apparent barriers. All the other species studied appear to be in intermediate stages of evolutionary divergence. The members of group 2, *E. terrestris* and *E. bormansi*, are evidently highly related taxa. No reproductive barrier whatsoever appears to exist between them. Nadig (1980) considers *E. bormansi* to be a subspecies of *E. terrestris* and described three vicarious subspecies, viz., *E. terrestris terrestris*, *E. t. bormansi* and *E. t. caprai*. Our data do not contradict his opinion. Nadig

(1980), furthermore, describes an extensive hybridisation zone in the south western part of the French Alps, which he considered to result from secondary intergradation. Nadig's hybridisation zone extends in the east-west direction from the French-Italian border to Grasse, that is, over a range of more than 50 km. Genetical information should be collected to verify this hypothesis. More morphometric data are being collected. Research on the allozymic variation in the various populations studied is in progress. It is hoped that the independent elaboration of "genetic distances" will elucidate the phylogenetic history. This applies also to the position of the species of the third group: *E. ephippiger* which is widely spread over Europe with a number of vicarious subspecies. The other species in this group are endemic ones with restricted areas, one (*E. cruciger*) being a lowland species, the other one (*E. cunii*) a mountain species.

With regard to the systematic status of the three species within this group, Voisin (1979: 127) stated that it is really impossible to distinguish *E. cruciger*, *E. cunii* and *E. ephippiger* and he cites Delmas (in litt.) that transition zones exist where hybridisation might occur. According to Voisin (1979: 127) many species and subspecies have been previously described, which are not more than local forms. Therefore, Voisin tends to lump the three species together into one very polymorphic species, *E. ephippiger*. Our data do not support this proposition: mating barriers do appear to exist between the three species (and also between *E. e. vitium* and *E. e. vicheti*), although these are generally not absolute.

Probably this situation could best be characterised by regarding group 3 as a superspecies: a monophyletic group of essentially allopatric species that are too different to include in a single species (Mayr, 1970). Speciation appears to have proceeded furthest in those two taxa (*E. cunii* and *E. cruciger*) that are adapted to habitats that differ rather largely from the general habitat *E. ephippiger* inhabits. Probably all members of the third group have the status of semispecies, because their process of speciation is not fully completed. Gene exchange is still possible among them but this is usually prevented by geographic isolation (Mayr, 1970).

#### SUMMARY

In a number of (sub)species of *Ephippiger* from southern France, Switzerland and north-

ern Italy, observations have been made on the occurrence of interspecific matings in no choice combinations. Secondly, (sub)species differences in the morphology of genital parts (cerci, epiproct, titillators, female subgenital plate) and in behaviour have been described. Thirdly, the geographical distribution is dealt with, specially emphasising the available data on partially overlapping distribution.

An interpretation of the data is presented and three groups are distinguished, between which no mating is possible:

group 1: with *E. provincialis*, forming the only example among the species studied of completed speciation;

group 2: including the species *E. terrestris* with (in accordance with Nadig, 1980) three subspecies, *E. t. terrestris*, *E. t. bormansi* and *E. t. caprai*; no mating barriers between these subspecies appear to exist;

group 3: forming something like a superspecies, including *E. ephippiger vitium*, *E. ephippiger vicheti*, *E. cunii* and *E. cruciger*; some mating barriers appear to exist between these species and subspecies, but these are not generally absolute.

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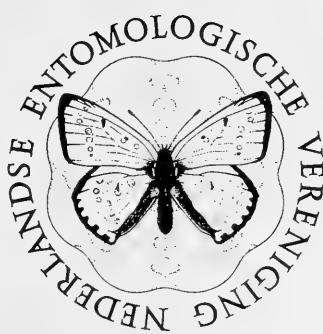
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# TIJDSCHRIFT VOOR ENTOMOLOGIE

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## INHOUD

H. H. EVENHUIS and H. J. VLUG. — The hymenopterous parasites of leaf-feeding apple tortricids (Lepidoptera, Tortricidae) in The Netherlands, pp. 109—135,  
figs. 1—103.



# THE HYMENOPTEROUS PARASITES OF LEAF-FEEDING APPLE TORTRICIDS (LEPIDOPTERA, TORTRICIDAE) IN THE NETHERLANDS

by

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## ABSTRACT

Fifty-six Hymenopterous parasites, reared from apple leafroller caterpillars and pupae in the Netherlands, are listed. Brief descriptions and a key are given to separate related parasite species. The great difficulties encountered in discriminating between narrowly related, insufficiently described species are discussed. These difficulties in most cases make it impossible to obtain reliable species names. Data about host specificity are given because identification of host caterpillars and pupae now became possible. Knowledge of host specificity is considered an essential and often indispensable aid in species discrimination.

## INTRODUCTION

In the Netherlands leafroller caterpillars belong to the most important apple pests. In particular *Adoxophyes orana* is harmful, though caterpillars of *Archips rosana*, *A. podana*, *Pandemis heparana*, *P. cerasana*, *Spilonota ocellana* and *Hedya nubiferana* may also cause considerable damage to the fruits.

The role that natural enemies play in controlling apple leafrollers is appreciated in quite different ways. Whereas Janssen (1958) does not consider the parasites of *Adoxophyes orana* essentially important in Western Germany, Auersch (1960) states that they contribute to a considerable reduction of its host numbers in the same region.

In connection with investigations on integrated control in apple growing, it was necessary to study the parasites of apple leafrollers. This means in the first place an inventory of the several parasites, together with investigations on the relationships with their hosts, and estimates of their importance as mortality factors of the leafrollers.

A number of papers concerning the parasite fauna of apple leafrollers in Europe have been published, viz., by Lehmann (1969), Papp & Reichart (1973), Carl (1974), Charles (1974), Evenhuis (1974a, b) and Miczulski & Koślinska (1976) for the D.D.R., Hungary, Switzerland, France, the Netherlands and Poland, respectively. These regions have many species in common, but also show differences. This may be largely caused by different identifications for one and the same species.

There is an urgent need for a reliable species identification of both parasites and hosts. It is a prerequisite to study their interrelationships and to compare the results with other regions. We will discuss these matters in the next chapters.

## METHODS

Leafroller caterpillars and pupae were collected from apple in various orchards in the Netherlands from 1970 onwards. Each specimen was separately kept in a glass vial under outdoor conditions and the caterpillars were provided with an artificial diet as recommended by Ankersmit (1968). They were inspected three times a week.

The emerging adult insects were either leafroller moths or Hymenopterous or Dipterous parasites. The Hymenoptera were glued on a triangular card board. The host caterpillar remains with the parasite cocoon were glued on a separate card board on the same pin. We took care to show the inner sides of the caterpillar mandibles, as these present important characters (Evenhuis & Vlug, 1972). Egg parasites are excluded from this study.

## IDENTIFICATION OF THE HOST

Though identifying adult Dutch Tortricidae does not give too much trouble, thanks to the works of Hannemann (1961), Bentinck & Diakonoff (1968) and Bradley et al. (1973), identification of the caterpillars and pupae is much more of a problem. The older living instars of the apple leafroller caterpillars may be identified with the key of De Jong & Vlug

(1974), based on superficial characters, particularly colours. Swatschek (1958) in his keys of last-instar caterpillars of Central European leaf-rollers mainly used the position of the chetae on thorax and abdomen as differentiating characters (chaetotaxy). However, after a parasite has emerged and the host caterpillar has died, the less sclerotized parts of the body appear too much shrivelled and discoloured to make a reliable identification possible.

We have been looking for characters that would better suit our particular needs. We consider the shape of the teeth of the retinaculum in the last three instar caterpillars of Tortricidae Tortricinae important in this respect (Evenhuis & Vlug, 1972). This character, however, seems to hold only for the identification of the genera. Thus genera with only one species occurring on apple, e.g., the most important *Adoxophyes orana*, do not give particular difficulties. In genera with two or more species on apple, these species may be often distinguished by colour differences in the more sclerotized parts as head and pronotum. The caterpillars of the three species of Tortricidae Olethreutinae occurring on apple, viz., *Spilonota ocellana*, *Rhopobota naevana* and *Hedya nubiferana*, are in the older instars, even in a shrivelled condition, generally sufficiently characteristic to be recognized.

Though we were not able to distinguish between the leafroller species in the first and second larval instars, this is hardly necessary as, till yet, we only reared parasites from the older instars.

As to the retinacular teeth we may state now that this character has turned out to be more useful than we suggested in our 1972 publication. Abrasion of the teeth seems only an exception.

A number of parasites emerged from leafroller pupae. Identification of pupae gives less problems than that of the caterpillars. A key for the Dutch species has been published (Evenhuis, De Jong & Vlug, 1973).

#### IDENTIFICATION OF PARASITIC HYMENOPTERA

The present paper is an attempt to name the Hymenoptera species that we reared from apple leafrollers. When possible, specialists were consulted; for the rest we tried to find out names ourselves. These names, of course, remain doubtful as long as the groups to which the species in question belong, have not yet adequately been revised.

Descriptions are given in which attention is

paid to the characters we consider important for species discrimination, especially in those species about the identity of which we are in doubt. We tried to find new morphological characters. When closely related species for comparison were lacking, we assumed that certain morphological structures might represent good characters. We hope then that during a later revision of the taxonomical groups in question the identity of those species might be established.

For the several species a discussion on host specificity and the period of emergence of adults according to our investigations are given. In table 1 data about host ranges are represented.

The drawings were made by the junior author.

#### Family ICHNEUMONIDAE

In Europe this may be the largest insect family. Perkins (1959) estimates the number of British species at 2000. The number of Dutch species is estimated to be of the same order of magnitude (Van Achterberg, 1982).

In the sequence of subfamilies, tribus and genera, as well as for the taxonomic terminology, we follow Townes (1969—1971), with some necessary alterations in the names.

#### Subfamily PIMPLINAE (= Ephialtinae, sensu Townes, 1969)

##### **Scambus brevicornis** (Gravenhorst) (figs. 1—4)

Colour characters. — Female. Head black, except for maxillary and labial palps which are yellowish; antenna dark brown. Thorax black, tegula yellowish white, coxae and legs light brown, middle tibia sometimes with subproximal dark ring or spot; hind tibia whitish, subproximally and distally with dark ring; hind tarsus whitish, with distally darkened segments. Abdomen black.

Male. Differs from female in having scape and pedicel whitish yellow below. Fore and middle coxae whitish yellow, rest of fore and middle legs yellow, the latter without dark tibial ring or spot; hind coxa for the most part black, hind trochanter yellow. The smaller males are on the whole somewhat lighter.

Morphological characters. — Female. Clypeus membranaceous and excavated (fig. 1). Prothorax smooth, shiny; mesoscutum and scutellum finely punctate and pilose; remainder of thorax more strongly pilose; propodeum with two incomplete longitudinal carinae, sparsely pilose in front outside the carinae, laterally longer and more densely pilose. Fore wing with small, rhombic areolet; hind wing with nervellus broken beneath the middle (fig. 2). First tergite with two distally converging carinae, area be-

tween them smooth in front, shiny, remainder roughly punctate and somewhat transversely wrinkled; remaining tergites rather strongly punctate, except for the narrow hind parts of segments 2, 3, 4, and 5, which are finely striated transversely (fig. 3); ovipositor two times the length of hind tibia, lanceolate and serrate ventrally near tip (fig. 4).

Male. Smaller and narrower than female. Carinae of propodeum sometimes extending to hind border. Narrow hind parts of tergites smoother, almost without transverse wrinkles.

Length female: 5—7 mm, ovipositor: 3—4 mm, length male: 3.5—5.5 mm.

The genus *Scambus* has not been revised in a modern way and this makes species identification doubtful. We use the name *brevicornis* because its description, together with Schmiedeknecht's interpretation (1914), apparently is closest to it. How intricate matters are, may be inferred from Schmiedeknecht's remark (1914): "Die Gruppe der P. [Pimpla, in which *Scambus* at that time was incorporated] *brevicornis* ist die schwierigste der ganzen Gattung. Wir stossen hier auf eine ganze Reihe in Habitus und in der Färbung verschiedener Formen, deren Abgrenzung als Art oder Varietät unübersteigliche Schwierigkeiten bereitet. Ich glaube nicht einmal, dass sorgfältige Zuchtvorschüsse viel Klärung beitragen würden, denn wollten wir die aus den einzelnen Wirten gezüchteten Formen als besondere Arten auffassen, wo wäre dann das Ende".

We quote Schmiedeknecht's opinion especially because of his misuse of the species concept. A species has to be considered a reproductive community. Only this species concept may be handled in ecological investigations, like that of apple leafroller parasites. As time-consuming cross breeding experiments cannot be easily performed, taxonomists have to rely upon morphological and colour characters from which they usually do not know the variation limits. In contrast to Schmiedeknecht's view, we think that rearing parasites from well-known hosts is always a great help in fixing this variability.

Ohlke (1965) reports *Scambus brevicornis* to be reared from the sawfly *Neodiprion sertifer*; he further mentions the species as a primary parasite of several Microlepidoptera, Diptera and of *Anthonomus pomorum* (Coleoptera). If these records are indeed reliable, *Scambus brevicornis* might be considered pantophagous.

"*Scambus brevicornis*" in our investigations was reared in large numbers as a solitary ectoparasite of second generation *Adoxophyes orana* caterpillars in well-kept orchards. However, the

first instar parasite larva seems to live endoparasitically; the larval moult may be seen protruding from the caterpillar skin. It was observed together with the gregarious ectoparasitic larvae of *Colpoclypeus florus*, which is much more common. The parasite larvae feed on dead caterpillars, just like those of *C. florus*. We do not know if any ecological relation between the two parasitic species exists.

Adults: 24 July—28 September. A single specimen appeared on 24 April next spring.

#### *Itoplectis alternans* (Gravenhorst) (figs. 5, 6)

Colour characters. — Female and male. Black. Antenna brownish beneath, maxillary and labial palps light brown. Legs predominantly brown, coxae black, hind tibia light and dark brown with a white subbasal ring, tarsal segments of hind leg dark brown, proximally white except for the short fourth one; all claws dark.

Morphological characters. — Female and male. Body for the greater part pubescent. Antenna long, extending far beyond middle of abdomen; inner margin of eye distinctly excavated above the middle, face finely and widely punctate, with short, thin hairs (fig. 5). Mesoscutum rather finely punctate, covered with short, fine hairs, distance between punctures much larger than their diameters; propodeum with two incomplete longitudinal carinae, shiny, bare, except for the pubescent outer front corners. Fore wing with small, rhombic areolet; hind wing with nervellus broken considerably above the middle (fig. 6). Tergites roughly punctate, first smooth between the two lateral carinae in front; tergites 6 and especially 7 more finely punctate than the preceding ones.

Length female: 4.5—7.5 mm, ovipositor: 1—1.5 mm, length male: 2.5—8 mm.

We reared this species as a primary parasite from the pupae of several leafroller species and as a secondary parasite from cocoons of other leafroller parasites. It is known as a primary parasite of the pupae of Lepidoptera belonging to several families and also as a hyperparasite of Lepidoptera through other primary Hymenopterous parasites. Perkins (1957) mentions seasonal dimorphism in the male that we could not confirm.

Adults: 15 August—16 September.

#### *Itoplectis maculator* (Fabricius) (fig. 7)

Morphological and colour characters. — This species resembles the former in many respects. Differences are given by Perkins (1941). The hairs on head and thorax are longer and the punctuation is stronger. This is especially shown on the face (fig. 7) and the

middle of the mesoscutum; on the latter the diameter of the punctures is about equal to the distance between these punctures, whereas in the preceding species this distance is much larger. There are also a number of colour differences, the hind borders of the middle tergites and in the female also the lateral borders being brownish.

Length female: 5.5—9 mm, ovipositor: 1.5—2.5 mm, length male: 5.5—7.5 mm.

Though we reared this species in somewhat smaller numbers than the preceding one, it does not seem to be a rare parasite of apple leafroller pupae. We reared it from *Pandemis heparana*, *Adoxophyes orana*, *Archips rosana* and *Hedya nubiferana*. We also reared it from a parasite cocoon, probably *Meteorus ictericus*, on apple; the leafroller remains were lost, however.

Adults: 21 August—1 October. One specimen appeared on 18 July.

#### *Apechthis* spp. (figs. 8, 9)

We reared only a few specimens, belonging to three species of this genus, from apple leafroller pupae. Just like in the related genus *Itoplectis*, the inner margin of the eye is distinctly excavated (fig. 8). However, in contrast with this genus, the head shows distinct yellow markings and the ovipositor is bent downwards (fig. 9).

With the keys of Perkins (1941) and Kasparyan (1973) the species could be identified as *Apechthis compuncator* (L.), *A. quadridentatus* (Thomson) (= *A. resinator* Thunberg), and *A. rufatus* (Gmelin). Our rearings yielded one male of *A. compuncator* from *Hedya nubiferana* (collected as pupa on 24 June), one female of *A. quadridentatus* from *Pandemis heparana* (adult on 3 August), and two males of *A. rufatus* from *Archips rosana* and *Ptycholoma lecheana*, respectively (adults on 29 and 30 June).

Considering the small numbers reared, it is of no use going into further details.

#### Subfamily TRYPHONINAE

##### *Phytodietus segmentator* (Gravenhorst) (figs. 10, 11)

Colour characters. — Female. Black, with small, yellow markings above, especially on scutellum, postscutellum and propodeum. Antenna brownish, above proximally black. Legs predominantly rufous. Hind borders of tergites to a varying extent yellowish.

Male. Yellow, above for the most part black, with rather extensive yellow markings. Antenna and legs as in female. Hind borders of tergites yellowish.

Morphological characters. — Female and male. See

figures of fore tarsal claw (fig. 10) and of wings (fig. 11).

Length female: 4.5—7 mm, ovipositor: 1.5—2.5 mm, length male: 5.5—7.5 mm.

We reared only a few specimens, from a number of localities, exclusively from larvae of *Archips*, both *Archips podana* and *A. rosana*. This species is recorded as a well-known parasite of *Tortrix viridana*. Horstmann (1971) reared it from *Archips xylosteana*, *A. rosana*, *Eudemis porphyrana* and in autumn from *Ancylis mitterbachiana* on oaks. Bogenschütz (1965) considers it an oligophagous parasite of Tortricidae. Horstmann regards it to be plurivoltine.

Adults: 29 June—5 July.

#### Subfamily CRYPTINAE (= Gelinae, sensu Townes, 1969)

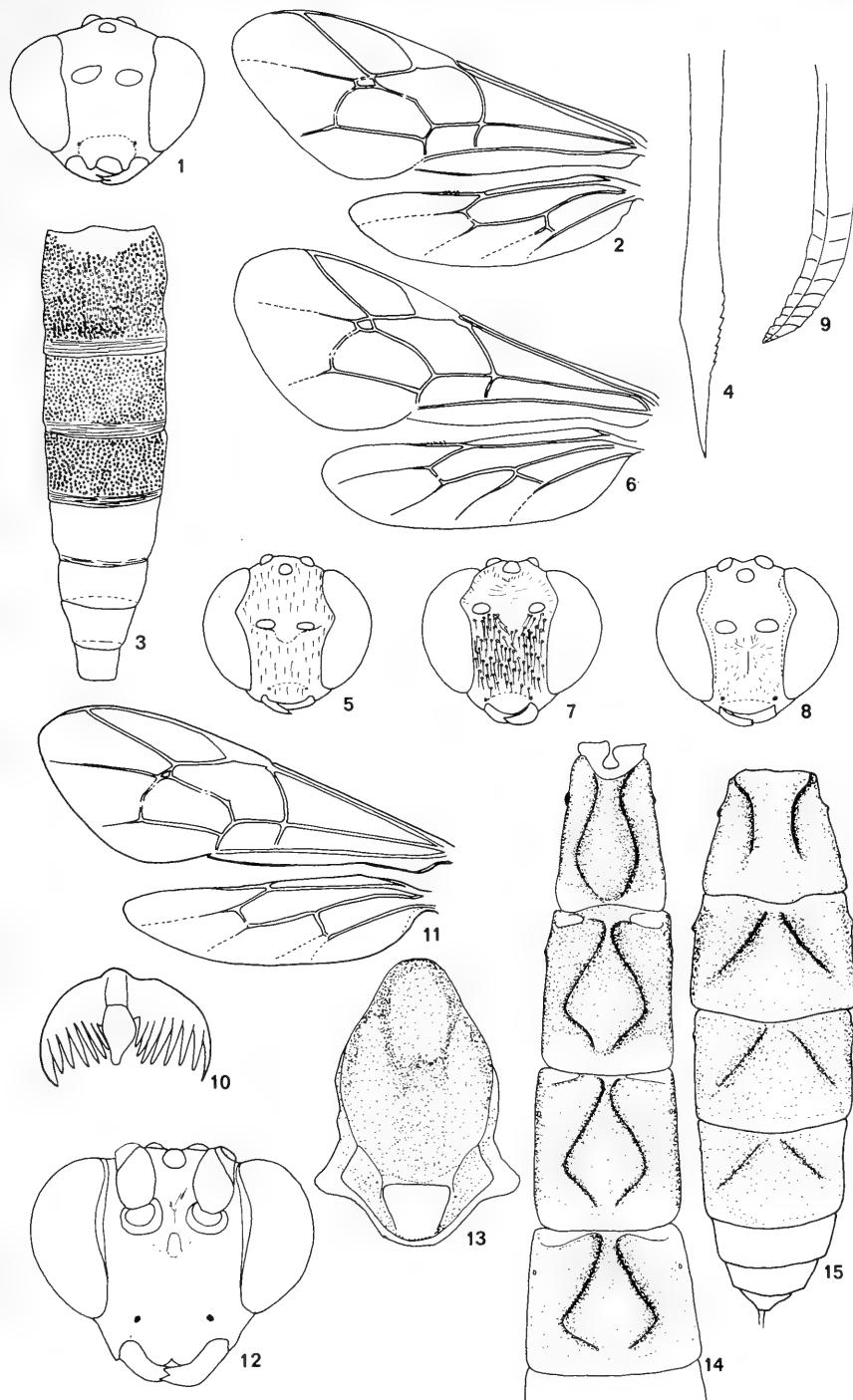
Members of this in taxonomic respect often so difficult subfamily were reared from apple leafrollers as hyperparasites in only very small numbers. They do not seem to play an important role in the natural control of apple leafrollers. Therefore we will only mention them without going into details.

We reared four specimens of *Gelis* sp., three from cocoons of *Porizontinae*, two of these from *Archips rosana*, and one probably from *Spilonota ocellana* as indirect hosts; one specimen was reared from a pupa of *Adoxophyes orana*. Furthermore, one specimen of *Acrolyta* sp. was obtained from *Spilonota ocellana* through some unidentified Braconid as a direct host, and a few specimens of *Lysibia nana* (Gravenhorst) from cocoons of the gregarious *Apanteles ater*, *Pandemis heparana* being the indirect host. The identifications were made by Drs. K. W. R. Zwart and Mr. G. van Rossem.

#### Subfamily BANCHINAE

The Glyptini, represented here by the genera *Teleutaea*, *Apophua*, and *Glypta*, are characterized by the presence of oblique furrows on the tergites 2, 3, and 4 (cf. figs. 14 and 15). We reared five species, viz., *Teleutaea striata* (Gravenhorst), two *Apophua* and two *Glypta* species. *Teleutaea striata*, the only species that was reared in considerable numbers from apple leafrollers, is easily known by its characteristic black and yellow markings.

Identification of *Apophua* and *Glypta* species provide considerable difficulties. There exists a modern revision by Aubert (1978), but identification with his key is a precarious business



Figs. 1—4. *Scambus brevicornis*: 1, head anteriorly; 2, wings; 3, gaster; 4, tip of ovipositor. Figs. 5—6. *Itoplectis alternans*: 5, head anteriorly; 6, wings. Fig. 7. *Itoplectis maculator*, head anteriorly. Figs. 8—9. *Apechthis quadridentatus*: 8, head anteriorly; 9, tip of ovipositor. Figs. 10—11. *Phytodietus segmentator*: 10, claw; 11, wings. Figs. 12—14. *Teleutaea striata*: 12, head anteriorly; 13, thorax dorsally; 14, first four tergites. Fig. 15. *Glypta varicoxa*, gaster dorsally.

which, in our species, was not always conclusive.

We think that head, pronotum and prepectal carina show sufficient differential species characters. These will be given in the following descriptions.

### **Teleutaea striata** (Gravenhorst)

(figs. 12—14, 89)

Colour characters. — Female and male. Preponderantly black. Clypeus, cheek beneath and mouthparts, except for the tips, yellow; antenna brown yellow. Pronotum along front margin partially and along hind margin entirely yellow. Tegula and small adjoining part of mesopleurum yellow, just like a large spot in front of middle coxa. Scutellum, postscutellum and posterior part of propodeum before the apical transverse carina yellow; coxae and legs yellow and yellowish red. Hind margins of the tergites yellowish. The extension of the yellow markings may vary considerably.

Morphological characters. — Female and male. Clypeus incised; a small unpaired tubercle before the insertion of the antennae (fig. 12). Parapsidal furrows distinct in front part of mesoscutum (fig. 13). Apical transverse carina of propodeum distinct, the other carinae absent. Abdomen, see fig. 14; second, third, and fourth tergites, especially in the male, sometimes with a longitudinal middle carina in the first third.

Length female: 7.5—12 mm, ovipositor 5—7.5 mm, length male: 8—12 mm.

This species, easily recognized by its colour pattern, was reared in large numbers from apple leafroller caterpillars, mainly from *Adoxophyes orana*, but also in small numbers from *Pandemis heparana* and *Ptycholoma lecheana*, however not from other caterpillars. There appear to be two generations which coincide with those of *Adoxophyes orana*, perhaps the reason that it appears especially adapted to this host.

Adults: 1 May—28 August. A single specimen emerged on 6 April.

### **Apophua cicatricosa** (Ratzeburg)

(figs. 16—19, 99)

Colour characters. — Female and male. Black. Clypeus and mouth-parts yellow; antenna brownish. Upper embossed rim and hind corner of pronotum yellow; tegula, tip of scutellum and hind border of postscutellum yellow; legs yellowish brown, hind femur distally and hind tibia and tarsus darker except in the female, where the hind femur is whitish and both subproximally and distally darker. One male had no yellow markings on the thorax, except for the hind corner of pronotum and the tegula.

Morphological characters. — Female and male. Clypeus broadly rounded, without incision in the middle (fig. 16); base of mandible 1.6 as long as the

shortest distance between mandible and eye; genal carina not strongly sinuated (fig. 17). Pronotal collar separated from the rest of the pronotum by a deep groove, the collar covering the propleurum entirely, thus not visible from above; epomia long, appearing as a sharp edge, reaching to near upper edge of pronotum (fig. 18). Propodeal carinae complete and strong, more or less variable. Spur of front tibia distinctly exceeding the middle of the first tarsal segment (fig. 19).

Length female: 10 mm, ovipositor: 5.5 mm (as long as hind tibia), length male: 10 mm.

We reared seven specimens, six from *Pandemis heparana* and one from *P. cerasana*.

Adults: June, July.

### **Apophua** sp.

This species, which we can not identify, resembles *A. cicatricosa* in many respects. Our single specimen, a female, differs from it by being somewhat larger, 11.5 mm, ovipositor 7 mm (two times length of hind tibia), having the carinae on the propodeum more oblique, and only the anterior part of the median longitudinal carinae and the costula being distinctly defined. It was reared from *Archips podana*.

### **Glypta nigrina** (Desvignes)

(figs. 20—23)

Colour characters. — Female. Black. Clypeus with indistinct yellow markings; antenna brown. Tegula yellow; hind tibia without distinct bands, inner side whitish.

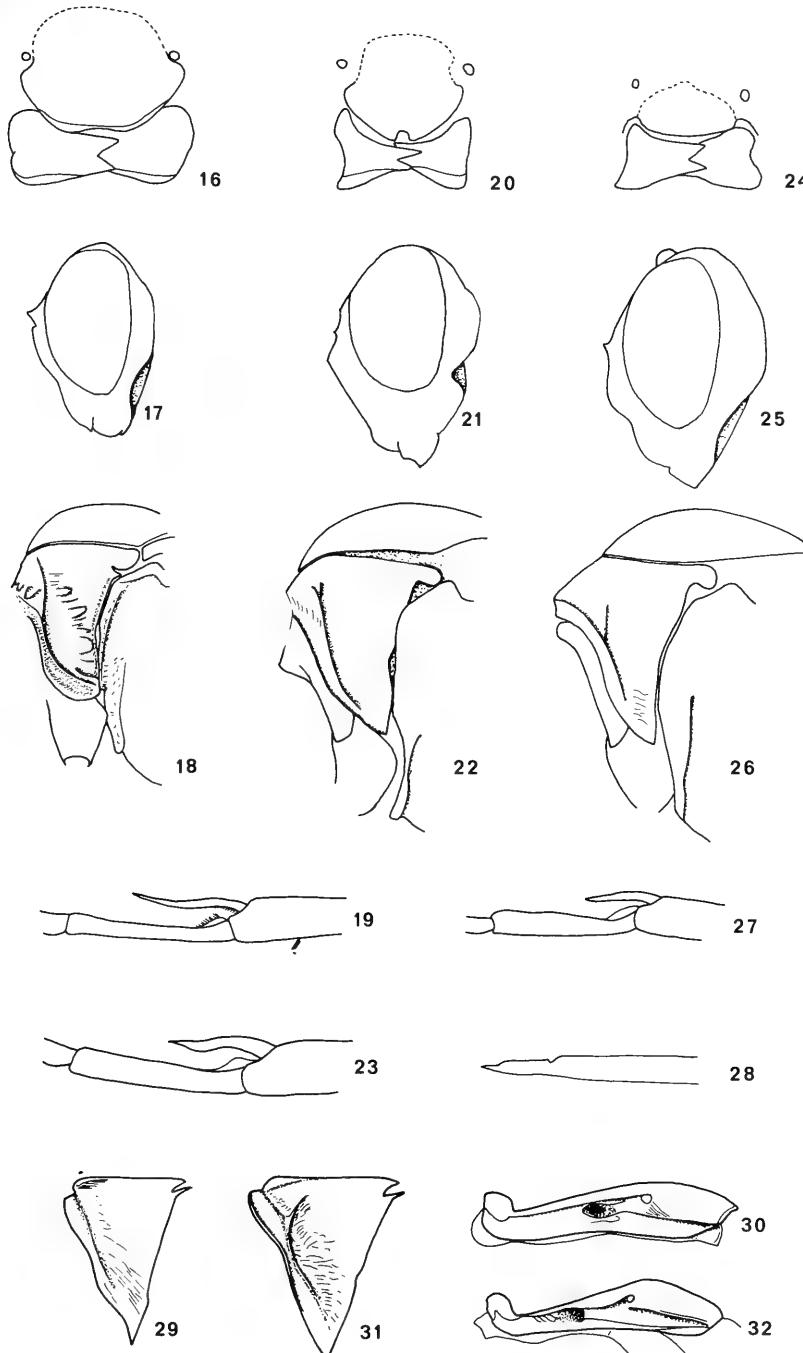
Male. As female, however clypeus yellow, its front border brownish.

Morphological characters. — Female and male. Clypeus narrow, rather convex, with small incision (fig. 20); base of mandible as long as shortest distance between mandible and eye; genal carina strongly sinuate (fig. 21). Pronotal characters similar as in *A. cicatricosa*, but less distinctly defined; collar narrower, showing lower part of propleurum, visible from above (fig. 22); pronotum rather uniformly scattered and coarsely punctate; mesopleural fovea absent. Spur of fore tibia not quite reaching middle of first tarsal segment (fig. 23).

Length female: 7—8 mm, ovipositor: 4—5 mm, length male: 8 mm.

This species seems quite similar to *Glypta varicoxa*, but may easily be distinguished by the structures of clypeus, genal carina and pronotum. Considering the length of the front tibial spur in this species, the separation between *Apophua* with the spur reaching to middle of first tarsal segment or beyond and *Glypta*, the spur not reaching to the middle, seems hardly justified.

We only reared two specimens from *Adoxo-*



Figs. 16—19. *Apophua cicatricosa*: 16, clypeus with mandibles; 17, head laterally, showing genal carina; 18, pronotum laterally; 19, tibial spur of fore leg. Figs. 20—23. *Glypta nigrina*: 20, clypeus with mandibles; 21, head laterally, showing genal carina; 22, pronotum laterally; 23, tibial spur of fore leg. Figs. 24—28. *Glypta varicoxa*: 24, clypeus with mandibles; 25, head laterally, showing genal carina; 26, pronotum laterally; 27, tibial spur of fore leg; 28, tip of ovipositor. Figs. 29—30. *Diadegma praerogator*: 29, pronotum laterally; 30, first tergite of abdomen laterally. Figs. 31—32. *Tranosema arenicola*: 31, pronotum laterally; 32, first tergite laterally.

*phyes orana* and two from *Ptycholoma lecheana*.

**Glypta varicoxa** Thomson  
(figs. 15, 24—28, 90)

Colour characters. — Female and male. Black. Clypeus dark brownish, palps yellow, antenna brownish. Hind corner of pronotum yellow; tegula yellow; legs yellow and reddish yellow, hind tibia with subbasal and apical dark ring, hind tarsus with dark rings.

Morphological characters. — Female and male. Clypeus broadly rounded, more or less depressed in the middle, without median incision (fig. 24); base of mandible 1.5 as long as shortest distance between mandible and eye; genal carina only very shallowly sinuate (fig. 25). Pronotal collar parallel to front margin as in *Apophua cicatricosa*, but less distinct and not especially deepened between collar and front margin; propleurum visible, epomia short (fig. 26); pronotum more or less uniformly punctate, without smooth or even weakly punctate middle part; spur of front tibia not reaching to middle of the first tarsal segment (fig. 27). Tergites 2, 3, and 4 with V-shaped impressions as in other *Glyptini* (fig. 15); ovipositor with apical, dorsal notch (fig. 28).

Length female: 6—7 mm, ovipositor: 4.5—5 mm, length male: 5.5—7 mm.

As far as apple leafrollers are concerned, this parasite seems specialized on *Spilonota ocellana*.

Adults: 28 June—17 July.

Though the characters mentioned by Aubert (1978) do not exactly fit our species, we provisionally maintain the name; it was mentioned earlier under the same name by Evenhuis (1974b). Perhaps *G. pedata* Devignes should be better. Both Charles (1974) and Couturier (1973) report to have reared a *Glypta* species from *Spilonota ocellana* on apple in France, which they name *G. pedata* and *G. (?) fractigena*, respectively. There can be little doubt that they refer to the same species as ours. *G. fractigena* is considered by Aubert a synonym of *G. nigrina* Desvignes. Thus either the species mentioned as *G. nigrina* in this paper, or the species stated under that name by Couturier, or perhaps both, might be misidentified. Further taxonomical investigations could elucidate these questions.

**Lissonota complicator** Aubert

This species was mentioned earlier as *Lissonota errabunda* Holmgren (Evenhuis, 1974b). According to Aubert's key (1978) it fits better into *Lissonota complicator*.

Colour characters. — Female. Black. Antenna dark brown, mouth-parts yellow. Fore and hind margins

and hind corners of pronotum yellowish brown. Legs red yellow.

Male. Conspicuously lighter coloured than female. Black. Antenna dark brown, scape and pedicel yellow below; a yellow spot between eye and outer ocellus on each side of frons; face and mouth-parts yellow, with black middle stripe extending from insertion of antennae downwards, not reaching front margin of clypeus. Front margin of pronotum lighter and with yellow spot on the outer hind corners; mesoscutum broad yellow on the front margin on each side, tegula yellow; legs red brown, fore and middle coxae and trochanter whitish yellow, hind coxa darker, hind tibia distally and first three segments of hind tarsus darkened. Hind borders of proximal tergites lighter.

Morphological characters. — As Aubert (1978) gives predominantly colour characters and as we have no specimens of related species to compare, we should refrain from giving morphological characters.

Length female: 4.5—6.5 mm, ovipositor: 5 mm, length male: 4—5.5 mm.

We reared this parasite in rather large numbers from caterpillars of *Archips podana* on apple. It might be a rather strictly specialized parasite of this leafroller. However, we saw Swiss specimens reared from a caterpillar of *Pandemis cerasana* by Dr. A. Schmid, Nyon, Switzerland.

It is a gregarious larval endoparasite with varying ratios of females and males per host. From one single host caterpillar 3 to 8 parasites emerged with an average of 6.

Adults: 11 June—15 July.

Subfamily PORIZONTINAE

**Diadegma praerogator** (Linnaeus), (*Diadegma interrupta* (Holmgren) (Horstmann, 1973))  
(figs. 29, 30)

Colour characters. — Female and male. Black. Mouth-parts yellow. Tegula yellow; fore and middle coxae often partly yellow; fore and middle trochanter yellow; femora light brown, hind tibia yellowish white, with broad basal and apical dark rings, all tarsi light brown, distally darker, last tarsal segment especially dark.

Morphological characters. — See *Tranosema arenicola*.

Length female *D. praerogator*: 4—6.5 mm, ovipositor: 1—1.5 mm, length male: 3.5—5.5 mm.

This species is one of the most common parasites of apple leafrollers. We reared it from caterpillars of several leafroller species (cf. table 1). Till yet we did not rear it from caterpillars of other families of Lepidoptera on apple, representatives of which, however, were only collected in relatively small numbers. Neither does

Herting (1965) mention it from Geometridae and Noctuidae on apple. Thus we consider *Diadegma praerogator* as a parasite, specialized on Tortricidae.

Townes (1969) referred *Diadegma interrupta* to the genus *Tranosema* Förster. Horstmann in his type revision of the European *Diadegma* species, placed *D. interrupta* in the subgenus *Nythobia* Förster, which contains the extremely uniform majority of the *Diadegma* species. The latter of course seriously interferes with species identification. Often males cannot be identified at all, because important characters, as eventual notches in the hind borders of the posterior sternites and the length and shape of the ovipositor, refer to the female sex only.

Adults: 13 May—7 October.

We reared some more *Diadegma* species from apple leafrollers, but only in very small numbers. They were identified by Dr. K. Horstmann as *D. apostata* (Gravenhorst), and as *D. fenestralis* (Holmgren). Three further specimens could not be identified.

#### *Tranosema arenicola* (Thomson) (figs. 31, 32)

Colour characters. — Female. As in *Diadegma praerogator*, however legs entirely light brown, but fore and middle coxae darker brown or even partly black, hind tarsus darkened.

Male. As female, but fore and middle coxae light brown.

Morphological characters. — The morphological characters may be treated together with those of the other Porizontini. As their general appearance is rather alike, it seems useful to compare some of their differentiating characters here. In the three *Diadegma* species mentioned above, the epomia is lacking (fig. 29), whereas this is short but evident in *Tranosema arenicola* (fig. 31). The lateral carinae on the first abdominal segment, running from its hindborder forward, are evident in the three *Diadegma* species and pass distinctly beneath the spiracles (fig. 30); in *Tranosema arenicola* they stop distinctly quite near the spiracle (fig. 32). As two of the *Diadegma* species that we reared are not important as apple leafroller parasites at all, it will be enough to refer to the publication of Horstmann (1969) for the differentiating characters. Horstmann (1973) discussed the similarity of *Diadegma praerogator* and *Tranosema arenicola*.

Length female *T. arenicola*: 5.5—6.5 mm, ovipositor: 1.5—2 mm, length male: 4.5—5.5 mm.

*Tranosema arenicola* was quite often reared from several leafroller species, however, far the most from *Archips rosana*. It is a solitary, larval endoparasite.

Adults: 14 June—26 July. A single specimen hibernated; the adult appeared on 7 May.

#### *Campoplex* spp.

*Campoplex* is a very large genus, like so many genera of Porizontinae. It gives tremendous difficulties in species discrimination. No modern revision of the genus exists. Therefore, in most cases reliable identification is impossible. Because our material from apple leafrollers is only scanty, we do not want to go into details.

We obtained five specimens from *Pandemis cerasana*, *Adoxophyes orana* and *Acleris rhombana*, which were identified by Dr. K. Horstmann as possibly *Campoplex difformis* Gravenhorst. Six further specimens, no doubt conspecific and of which five were reared from *Spilonota ocellana*, could not be identified, just like 13 specimens, probably belonging to at least three species, reared from several leafroller species.

#### Subfamily MESOCHORINAE

According to Townes (1971) the species belonging to this subfamily are secondary parasites through Ichneumonidae, Braconidae, Tachinidae (Diptera) and probably other families as direct hosts. He does not give information on indirect hosts. It is not excluded that some species might be primary parasites.

We reared only four specimens, a male and a female of *Mesochorus silvarum* Curtis and two males of *Stictopisthus lineatus* Thomson (det. Prof. Dr. W. Schwenke). The two specimens of the former species were reared from the caterpillars of *Pandemis cerasana* and *Adoxophyes orana*, respectively. The two specimens of the latter species were reared from a cocoon of probably *Meteorus ictericus* (Braconidae) without caterpillar host remains, and from a caterpillar of *Adoxophyes orana*, respectively.

#### Subfamily METOPIINAE

We reared only a few specimens of this subfamily, belonging to four species. They can easily be recognized, especially by their smooth body and the conspicuously short and stout legs (fig. 96); they are all larval-pupal parasites.

#### *Triclistus* Förster

The western palaearctic species have been dealt with by Aeschlimann (1973). Our material contains two species, that were identified by Dr. Aeschlimann as *Triclistus pallipes* Holmgren and *Triclistus globulipes* (Desvignes).

**Triclistus pallipes** Holmgren  
(figs. 33, 34, 96)

Ten specimens of this species, all females, were reared exclusively from *Rhopobota naevana*. Aeschlimann (1973) mentions *Strophedra weirana* (Lepidoptera, Tortricidae) as a host, which species is associated with *Fagus* and *Carpinus*.

Adults: 16 May—15 June.

**Triclistus globulipes** (Desvignes)  
(figs. 35—37)

Morphological characters. — Figures 33—36 show differences in the form of the head and in the pattern of pubescence on the gaster in both *Triclistus* species. Fig. 37 shows the propodeum of *T. globulipes* with the longitudinal carinae.

Of this species we reared two females, *Archips podana* being the host, and one male from *Archips xylosteana*. Aeschlimann (1973) mentions five more Tortricid host species.

Adults: 7 July—9 August.

**Exochus** Gravenhorst

We reared two species, each represented by one specimen, from pupae of *Clepsis spectrana* and *Acleris rhombana*. As there is no modern revision of the genus, it is not possible to name the two species.

**Exochus** sp. 1  
(fig. 38)

Colour characters. — Black. Head and mouth-parts, except ocellar area, bright yellow; scape black and yellow, rest of antenna brown, underside lighter. Thorax conspicuously marked with yellow; legs bright yellow, hind femur basally and apically black.

Morphological characters. — See *Exochus* sp. 2. Fig. 38 shows the propodeum with peculiarly shaped longitudinal carinae.

This species was reared from *Acleris rhombana*.

Adult: 7 July.

**Exochus** sp. 2

Colour characters. — Black. Antenna apically brownish, coxae and trochantera dark brown, remainder of legs lighter.

Morphological characters. — Differs from the former species in having basal vein less curved and having complete costulae.

This species was reared from *Clepsis spectrana*.

**Subfamily ANOMALONINAE**

The species of this subfamily are larval-pupal parasites. We reared only six specimens, belonging to two species. Two specimens of *Habronyx (Camposcopus) canaliculatus* (Ratzeburg) were reared from *Archips rosana*. Four specimens, belonging to *Agrypon anxiuum* (Wesmael), were reared from *Acleris rhombana* (three specimens) and from *Spilonota ocellana* (one specimen). The subfamily was recently treated by Gauld & Mitchell (1977).

Adults of *Habronyx canaliculatus*: 7 July—19 July. Adults of *Agrypon anxiuum*: 9 June—24 July.

**Family BRACONIDAE**

Reliable identification of the species of Braconidae that parasitize apple leafrollers seems only exceptional. The difficulties will be discussed in the special cases. As to the division into subfamilies we follow Van Achterberg (1976).

**Subfamily MICROGASTRINAE**

**Apanteles** Förster

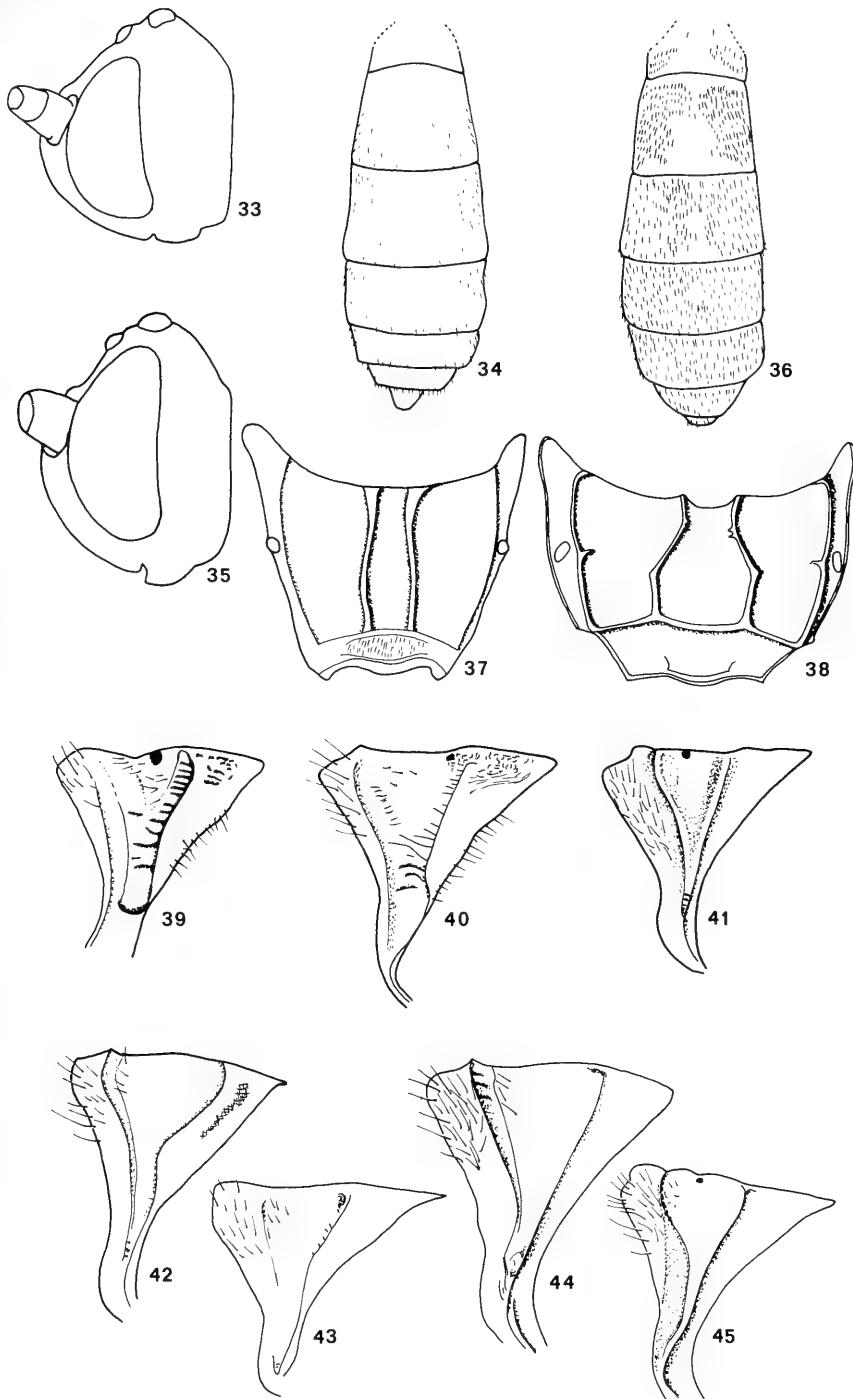
Two species of this very large genus, viz., *A. ater* (Ratzeburg) and *A. xanthostigma* (Haliday), may be considered the most important *Apanteles* species associated with apple leafrollers by far (Evenhuis & Vlug, 1973). Nixon (1965, 1973) gave a division in groups; in several publications he dealt with the species in detail (Nixon, 1972, 1973, 1974, 1976). Several groups of Nixon are treated as independent genera by Mason (1981).

We reared seven species from apple leafrollers. They may be distinguished especially by characters of the pronotum (figs. 39—45), of colouration of the pterostigma (figs. 46—52), of hind wing venation and of propodeum and tergite of the first gastral segment (figs. 53—59).

**Apanteles ater** (Ratzeburg)  
(figs. 39, 47, 53, 60)

Colour characters. — Female and male. Preponderantly black. Mouth-parts, distal part of fore femur, fore tibia, fore tarsus, base of middle tibia, middle tarsus and all tibial spurs lighter. Wing veins for the greater part pale, however costal vein and pterostigma distinctly pigmented; the parts of 2r proximally of Rs and short distal part of M less distinctly pigmented; pterostigma brownish yellow in the center, margins darker (fig. 47).

Morphological characters. — Female and male. Propodeum with two distinct carinae, converging in



Figs. 33—34. *Triclistus pallipes*: 33, head laterally; 34, gaster dorsally. Figs. 35—37. *Triclistus globulipes*: 35, head laterally; 36, abdomen dorsally; 37, propodeum. Fig. 38. *Exochus* sp. 1: propodeum. Figs. 39—45. Microgastrinae spp., pronotum laterally: 39, *Apanteles ater*; 40, *A. xanthostigma*; 41, *Dolichogenidea sicaria*; 42, *D. laevigata*; 43, *D. corvina*; 44, *D. dilecta*; 45, *D. longicaudus*.

front and thus forming a V, a little coarse, but smooth and shiny between and just outside the keels. First tergite twice as long as broad, the sides rather strongly converging distally (fig. 53). Ovipositor valves about as long as hind tibiae.

Length female: 2—2.5 mm, ovipositor: 0.5—1 mm, length male: 2—2.5 mm.

Nixon (1976) states that this species is poorly characterized as a whole, but that it is easily recognizable in the female by the presence of a fine, curved spine on the ventral side of the last tarsal segment of the front leg (fig. 60).

This species has been treated by Wilkinson (1945) in such an accurate way, that we have no doubt about its identity. This author also studied Ratzeburg's type material. The species was originally described as *Microgaster carbonarius* Ratzeburg, 1848, but later on renamed *Microgaster ater* Ratzeburg, 1852, as the former name appeared to be preoccupied by *Microgaster carbonarius* Wesmael, 1837.

Ratzeburg (cf. Evenhuis & Vlug, 1973) states about the host: "Von mir aus versponnenen Apfelblüthen erzogen, wahrscheinlich aus der brumata, die diese versponnen hatte". However, the host may as well have been some species of Tortricidae instead of *Operophtera brumata*. Wilkinson states the parasite to have been reared from *Cacoecia* (= *Archips*) *podana*, *Hyponomeuta malinella* (= *Yponomeuta malinellus*), *Tortrix* (= *Lozotaenia*) *forsterana*, *Noctocelia udmanniana*, and a specimen from a leaf-roller of *Ribes nigrum*. From this enumeration only *Yponomeuta malinellus* does not belong to the Tortricidae. It does not seem improbable that the mention of this host is due to a mistake, as *Yponomeuta* caterpillars live gregariously in large nests and some Tortricid host caterpillar may have been mixed with them.

According to our opinion *Apanteles ater* must be considered a specialized parasite of the caterpillars of various Tortricidae. However, the species seems to show some preference for the larger caterpillars. We reared rather many specimens, almost exclusively from *Archips podana* and *Pandemis heparana*, but only a few from *Adoxophyes orana*, *Ptycholoma lecheana*, and *Acleris* spp.

This is the only gregarious species within the genus that we reared from leafrollers associated with apple. Like other *Apanteles* species it is a larval endoparasite.

Adults: 25 May–18 September.

### *Apanteles xanthostigma* (Haliday) (figs. 40, 46, 54)

This species is very similar to the preceding one, both in colour and in morphological respect.

Colour characters. — Female and male. The species differs from *A. ater* by the centre of the pterostigma being more yellowish instead of white (fig. 46) and in the female sex by the legs being more extensively light-coloured.

Morphological characters. — Female and male. The most striking difference with the preceding species is, according to our opinion, the structure of the propodeum. This contains a longitudinal trough in the middle, which is at least distinct in its hind part and there bordered by short longitudinal carinae (fig. 54). The propodeum, on the whole, is also coarser. The female does not have a curved spine on the last tarsal segment of the fore leg.

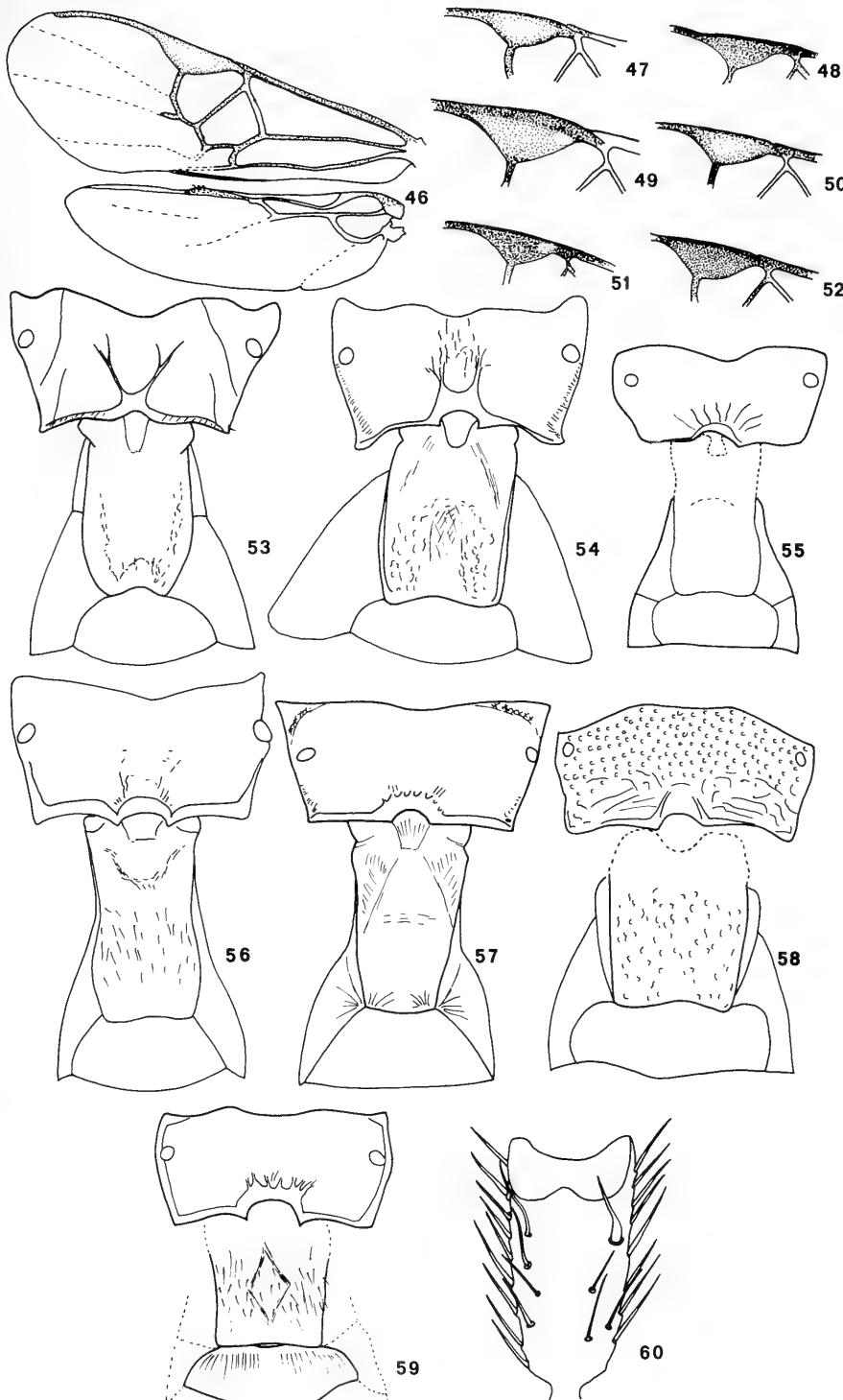
Length female: 2.5—3 mm, ovipositor: 0.5—1 mm, length male: 2.5—3 mm.

The species has been dealt with by Nixon (1976), who mentions a number of hosts, belonging to several families of Microlepidoptera. Telenga (1955) also enumerates the hosts, belonging to various Lepidopterous families. Zwölfer (1962) characterizes its host preference as follows: „Die von uns seit einigen Jahren untersuchte, recht polyphage Braconide *Apanteles xanthostigma* Hal. beschränkt ihr Suchgebiet praktisch auf die Strauch- und Baumschicht, greift hier aber eine grösse Zahl von Wirten, meist Wickler und verwandte Kleinschmetterlingsgruppen an“.

We reared a large number of specimens from several leafroller species of apple (cf. table 1), but we have no experience with the hosts of other Lepidopterous families. If indeed only one and the same species is involved, it might be considered a polyphagous parasite of Lepidoptera. *Apanteles xanthostigma* is a solitary endoparasite.

Adults: 13 May—8 September.

Besides the two species mentioned, we reared some more Microgastrinae, however in quite low numbers: *Dolichogenidea corvina* (Reinhard) from Nixon's "metacarpalis" group; *Dolichogenidea laevigata* (Ratzeburg), *D. dilecta* (Haliday), *D. sicaria* (Marshall) and *D. longicaudus* (Wesmael) from Nixon's "laevigatus" group. As these species have been dealt with thoroughly in taxonomical respect by Nixon



Figs. 46—60. Microgastrinae spp. 46, *Apanteles xanthostigma*, wings. 47—52, pterostigma: 47, *Apanteles ater*; 48, *Dolichogenidea sicaria*; 49, *D. laevigata*; 50, *D. corvina*; 51, *D. dilecta*; 52, *D. longicaudus*. Figs. 53—59. Propodeum and first tergites: 53, *Apanteles ater*; 54, *A. xanthostigma*; 55, *Dolichogenidea sicaria*; 56, *D. laevigata*; 57, *D. corvina*; 58, *D. dilecta*; 59, *D. longicaudus*. Fig. 60. *Apanteles ater*, last tarsal segment of fore leg of female ventrally.

(1972, 1973) and as they apparently do not play any important role in the natural control of apple leafrollers, it does not seem necessary to treat them here in detail.

Our material is far too poor to allow any conclusion as to their host specialization. In figs. 39—60, morphological details of the several *Apanteles* species are given, which may be sufficient to separate them.

Twelve further specimens of the subfamily Microgastrinae, all belonging to the genus *Lisogaster* Bengtsson (= *Microgaster* auct.), were reared. They belong to at least four species and apparently are not important as parasites of apple leafrollers.

Nixon (1965) states: "Taxonomically, *Microgaster* is in a state of confusion and with regard to European species, there has been no improvement on Thomson's treatment of the genus". Thomson's work appeared between 1869 and 1897!

#### Subfamily AGATHIDINAE

We reared only two species of this subfamily from apple leafrollers. Both species seem, at least within the host range that we investigated, restricted to *Spilonota ocellana* and are rather common solitary endoparasites. The subfamily may be easily recognized by the very narrow radial cell in the fore wing (fig. 64). Notauli deep in both species.

##### *Agathis dimidiator* (Nees)

(figs. 61—63)

Colour characters. — Female. Black. Mouth-parts yellow. Legs reddish yellow, often with somewhat lighter trochantera; hind coxa black or largely black; hind tibia in the distal two third more or less black, for the rest whitish, lighter as the remainder of the legs; hind tarsi and ultimate ends of fore and middle tarsi dark.

Male. As female, but second gaster segment conspicuously light.

Morphological characters. — Female. The most salient characters of this species are, in comparison with the next one, the head elongated downwards slightly (fig. 61) and the first and generally the second tergite being partly rather coarsely striated longitudinally (fig. 62).

Male. As female, but striae on second tergite largely varying and in some cases even lacking (fig. 63).

Length female: 4—4.5 mm, ovipositor: 3.5 mm, length male: 4—4.5 mm.

The characters given here, borrowed from Telenga (1955) who placed the species in the ge-

nus *Microdus* Nees, are rather doubtful. A revision of this genus and allied genera seems urgent. Until so far we shall use the species name *dimidiator*, quoted from Telenga (1955).

As stated above we reared this species only, but rather commonly, from *Spilonota ocellana*. Telenga (1955) mentions *Archips rosana*, *Croesia bergmanniana* and *Epinotia tetraquetrana* as hosts, all Tortricids.

Adults: 4 July—13 August.

##### *Agathis rufipes* (Nees) (*Braunsia rufipes* (Nees)) (in Telenga, 1955)) (figs. 64—66)

Colour characters. — Female and male. Black. Mouth-parts, tegula and legs reddish yellow, except for the extreme distal end of the hind tibia and the greater part of the hind tarsus; tibial spurs all more or less whitish.

Morphological characters. — Female and male. As in the former species first radial and discoidal cells fused (fig. 64). Distal part of first tergite with fine longitudinal striation; base smooth, in contrast to the former species, where it is wrinkled all over its surface (figs. 65, 66); on each side a conspicuous, dorsolateral carina that does not reach the hind border, these carinae more lateral and thus inconspicuous in the former species. There are transverse grooves in the middle of each of the fused second and third tergites, so that it seems if one long tergite after the first tergite were divided into four sections by three transverse grooves; striation of first tergite continuing onto the first two sections.

Length female: 4—5 mm, ovipositor: 3.5 mm, length male: 4—5 mm.

This species superficially resembles the former in many respects, may, however, easily be distinguished from it by the colour of the hind legs and by the sculpture of the gaster, as mentioned.

We reared this species only from *Spilonota ocellana*, but rather commonly. Telenga (1955) mentions quite a lot of host species, which may at least be partly erroneous, especially where non-Lepidopterous hosts are involved. Betz & Schwerdtfeger (1970) mention one specimen that was reared from *Teleia luculella* (Lepidoptera, Gelechiidae) on oak.

Adults: 29 June—30 July. A single specimen appeared on 8 June.

#### Subfamily CHELONINAE

From this subfamily we reared only two *Ascogaster* species. Though both species superficially resemble each other very much, they may be easily distinguished. Just like other

members of the subfamily, as far as known, they are solitary egg-larval endoparasites.

**Ascogaster quadridentata** Wesmael  
(figs. 67—69)

Colour characters. — Female and male. Black. Scape for the greater part, rest of the antenna downside, trochantera, fore femur distally, and fore tibia reddish yellow; tibial spurs whitish yellow; middle leg in male often a little lighter, at least tibia proximally.

Morphological characters. — Female and male. Head with coarse sculpture, clypeus produced in a small angle (fig. 67). Thorax and abdomen with coarse sculpture, coarser than head, thorax coarsest (fig. 68). Horizontal front part and perpendicular hind part of propodeum distinctly separated; the boundary line with four strong teeth, from which the inner are a little smaller than the outer (fig. 69).

Length female and male: 3.5—4 mm.

The female lays the egg in the host egg, and the adult parasite emerges from the full-grown or almost full-grown caterpillar (Cox, 1932).

*Ascogaster quadridentata* seems specialized on Tortricidae Olethreutinae; the females of these moths lay their eggs separately on the host plants (Evenhuis, 1969, 1974). We reared this species commonly from *Spilonota ocellana* and *Hedya nubiferana*. It is a well-known parasite of *Laspeyresia pomonella*.

Adults: 19 June—24 July.

**Ascogaster rufidens** Wesmael  
(figs. 70—72)

Colour characters. — Female and male. Black. Mandible, palps, antenna basally downside, tegula, trochantera, femora and tibiae reddish yellow; middle of the tibiae and femora of the middle and hind legs a little darker; tibial spurs whitish yellow.

Morphological characters. — Female and male. Sculpture somewhat less coarse than in the preceding species. There are three small, reddish teeth on the lower border of the clypeus (fig. 70). Wesmael (1835) (see Fahringer, 1934) mentions this explicitly.

Length female and male: 3.5—4.5 mm.

These characters, combined with others mentioned by Wesmael in his detailed description, are sufficient to recognize the species. Characters of mesoscutum and propodeum, to be compared with those of *A. quadridentata*, are shown in figs. 71 and 72, respectively.

This species resembles the preceding one, but may be distinguished at once by the colour of the legs — preponderantly black in *A. quadridentata* and reddish yellow in *A. rufidens* — and by the structures of the propodeum.

In contrast to the former species, its hosts

seem restricted to the Tortricidae Tortricinae, which lay their eggs in batches. We reared many specimens, especially from *Pandemis cerasana* and *P. heparana*, but also often from *Adoxophyes orana*. Matthey (1967) reared the species from *Pandemis cerasana*, *P. coryana* and *Batodes angustiorana* on oak.

Adults: 25 May—21 July.

Subfamily EUPHORINAE

**Meteorus ictericus** (Nees)  
(figs. 73—75, 95)

Colour characters. — Female. Reddish yellow. Antenna and ocellar space darker. Often the whole thorax is entirely dark or even black, except for the greater part of the prothorax. In some specimens only the propodeum is dark and often the distal ends of the tibiae and the tarsi. Often the first tergites and the middle part of the last tergites are black, or the abdomen is almost completely black except for the fused second and third tergites.

Male. As female, but often a little lighter.

Morphological characters. — Female and male. In figs. 73, 74 and 75, thorax and the first three tergites are shown, which might be of interest in the separation of this species. The propodeum is more or less irregularly reticulated and shows some variability; in specimens reared from *Adoxophyes orana* it seems coarser than in other specimens. The first gastral segment shows longitudinal wrinkles and two dorsal pits (dorsope: van Achterberg, 1974).

Length female: 3.5—5 mm, ovipositor: 2 mm, length male: 3.5—4.5 mm.

According to Fischer (1970) a critical revision of the species of *Meteorus* belongs to the most difficult questions in the taxonomy of Braconidae. The genus as such may be easily recognized, but separation of the many species is often extremely difficult. In Fisher's key our species runs to *Meteorus ictericus*. A critical revision of the Palaearctic species is given by Huddleston (1980).

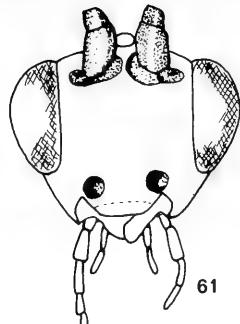
This parasite is one of the most common species that we reared from several apple leafroller species (cf. table 1).

Adults: 2 May—28 August. A single specimen appeared on 6 April.

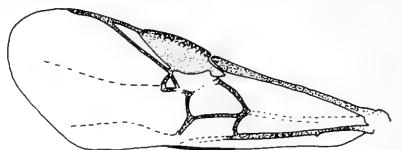
Subfamily ROGADINAE

**Oncophanes minutus** (Wesmael)  
(figs. 76—78)

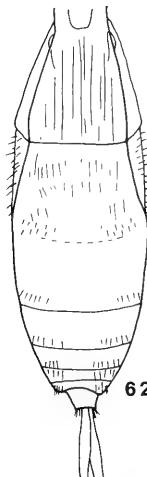
Colour characters. — Female. Body dark or even black. Basal part of antenna brown, mouth-parts, including palps, yellowish. Legs and ovipositor yellow. Pronotum partly, tegula and extreme superior part of



61



64



62



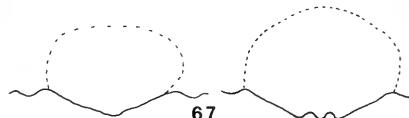
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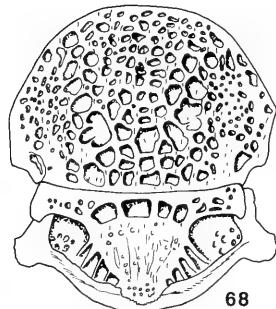


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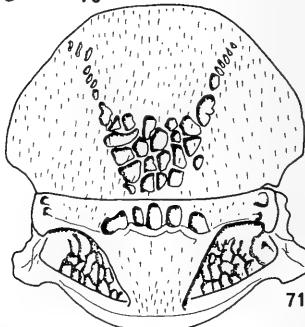


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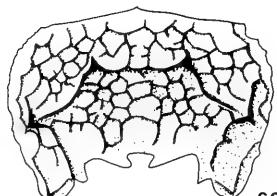
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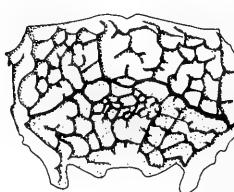
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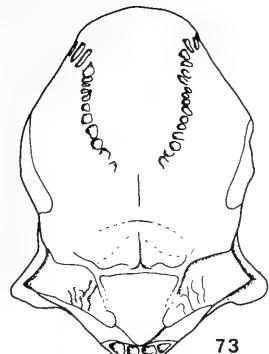


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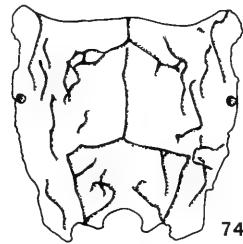


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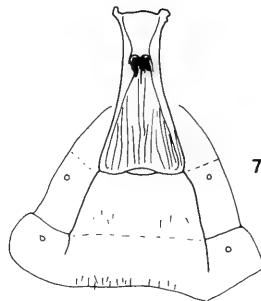
Figs. 61—63. *Agathis dimidiator*: 61, head anteriorly; 62, gaster female dorsally; 63, abdomen male dorsally. Figs. 64—66. *Agathis rufipes*: 64, wings; 65, gaster female dorsally; 66, gaster male dorsally. Figs. 67—69. *Ascogaster quadridentata*: 67, front edge of clypeus; 68, thorax dorsally; 69, propodeum. Figs. 70—72. *Ascogaster rufidens*: 70, front edge of clypeus; 71, thorax dorsally; 72, propodeum.



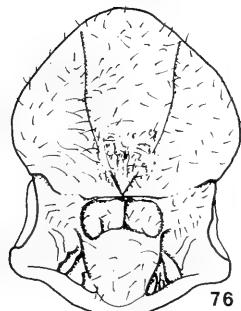
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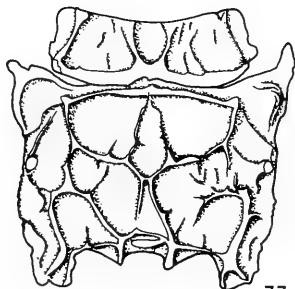
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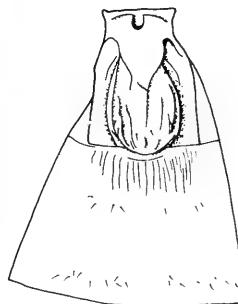
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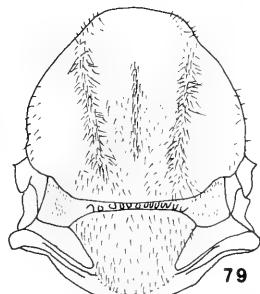
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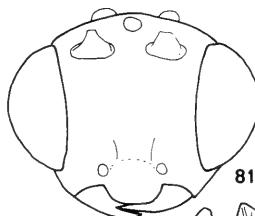
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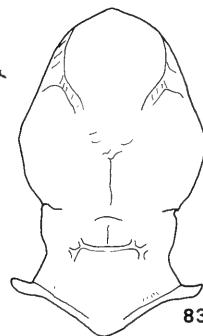
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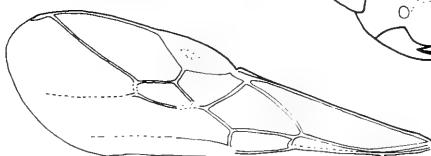
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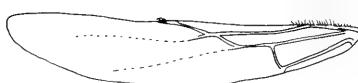
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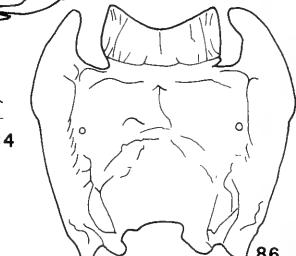
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Figs. 73—75. *Meteorus ictericus*: 73, thorax dorsally; 74, propodeum; 75, first three tergites. Figs. 76—78. *Onthophanes minutus*: 76, thorax dorsally; 77, propodeum; 78, first three tergites. Figs. 79—80. *Bracon* sp.: 79, thorax dorsally; 80, propodeum. Figs. 81—87. *Macrocentrus linearis*: 81, head anteriorly; 82, mandible; 83, thorax dorsally; 84, wings; 85, tarsal claw; 86, propodeum; 87, first three tergites.

mesopleurum reddish brown. Second tergite for the greater part yellowish.

Male. As female, but second tergite not as yellow.

Morphological characters. — Female and male. The exact difference between *Oncophanes minutus* and *O. laevigatus* (Ratzeburg) (= *O. lanceolator* (Nees)) is not clear from Fahringer's revision (1930). This is the last revision of the genus anyway! Occipital carina above fine, but distinct. Mesopleurum polished, but extreme superior part coarse. Mesoscutum sparsely covered with fine long hairs, parapsidal furrows evident (fig. 76). Propodeum with delimited areas (fig. 77). First tergite striated longitudinally, in front with two distally converging carinae, space between carinae smooth. Second and third tergites only separated by a shallow, in the middle almost faded transverse groove, second tergite longitudinally striated. The extension of this striation shows a rather large variability (fig. 78).

Length female: 2—2.5 mm, ovipositor: 0.5 mm, length male: 2 mm.

*Oncophanes minutus* is a gregarious ectoparasite. We reared it almost exclusively from *Adoxophyes orana* and only from a few localities. It must be considered an occasional parasite of apple leafrollers, without economic importance.

Adults: 6 August—26 August.

#### Subfamily HOMOLOBINAE

##### *Charmon cruentatus* Haliday

We reared only one specimen from a caterpillar of *Spilonota ocellana*. It was identified by Dr. C. van Achterberg, Leiden.

#### Subfamily BRACONINAE

##### *Bracon* sp.

(figs. 79, 80)

Among Braconidae *Bracon* is one of the largest genera. It is considered one of the most difficult genera of the Hymenoptera. A modern revision is lacking and sufficient reliable species characters are not known at the moment. There are many morphological differences between this species and the preceding one. We shall describe some that are most conspicuous, hoping that they may be an indication for the identity of the species, after the genus, eventually the group to which it belongs, has been revised.

Colour characters. — Female. Body dark, locally lighter, especially thorax and gaster downside.

Morphological characters. — Female. Mesoscutum smooth, with percurrent, converging notauli (fig. 79), which do not meet distally. Notauli shallow, with long setae, orientated mainly in two directions, inwards and outwards. Hind part of mesoscutum and

also scutellum densely pilose. Propodeum smooth, without areas (fig. 80). First tergite with two deep, distally converging grooves that enclose a triangular field.

Length female: 2.5 mm.

Of this species we only reared one female from *Adoxophyes orana*, which emerged on 12 August.

##### *Bracon obscurator* Nees

This species differs from the former by its smaller size and by the mesoscutum being much less pilose, the hairs on its hind part almost lacking. It was, provisionally, identified by Dr. C. van Achterberg.

Length male: 1.5—2 mm.

We reared two males from one caterpillar of *Spilonota ocellana*.

#### Subfamily MACROCENTRINAE

In this subfamily three *Macrocentrus* species were reared from apple leafrollers, mainly *M. linearis* (Nees), and a few specimens of the related *M. pallipes* (Nees) and one specimen of *M. thoracicus* (Nees). A modern revision of *Macrocentrus* is that of Eady & Clark (1964).

##### *Macrocentrus linearis* (Nees)

(figs. 81—87)

Colour characters. — Female and male. Preponderantly light brownish, however variable. Interoccellar space and a point on both sides of the insertion of the wings very dark to black. Upper side of thorax and gaster often dark in varying tinge and extension. Pterostigma dark centrally, with lighter margins (fig. 84).

Morphological characters. — Female and male. As morphological differences with related species have been dealt with by Eady & Clark (1964), we refer to that publication. We may add that the mesopleurum in this species is rather uniformly and widely punctate at its centre and not more densely in the furrow, which is only slightly pronounced; prepectal carina strongly curved (in *M. pallipes* the mesopleurum is irregularly punctate, and especially in the shallow, however pronounced furrow above the hind coxae densely punctate; prepectal carina straight). Figs. 81—87 show head, mandible, thorax above, wings, tarsal claw, propodeum, and first three tergites, respectively.

Length female: 4—5 mm, ovipositor: 6 mm, length male: 4—5 mm.

We reared this parasite often from *Pandemis cerasana*, *P. heparana* and *Archips podana*, thus from the larger leafroller caterpillars. After Eady & Clark (1964) the parasite has also been

reared from other Microlepidoptera than Tortricidae.

It is a gregarious larval endoparasite, apparently showing polyembryony. In most cases the progeny of one single host consists of either males or females exclusively. However, in a number of cases we reared both sexes from one single host, probably indicating that then at least two eggs were laid in a single host, giving rise to a female and a male progeny respectively.

Adults: 26 June—11 August.

#### **Macrocentrus pallipes** (Nees)

This species is very similar to the preceding one. Differentiating characters have been given by Eady & Clark (1964); a few supplementary characters were mentioned under *M. linearis*.

We reared 18 female specimens from one single caterpillar of *Hedya nubiferana*.

One specimen of *Macrocentrus thoracicus* (Nees) was reared from a caterpillar of *Spilonota ocellana*. It was, just like *M. linearis* and *M. pallipes*, identified by Dr. C. van Achterberg, Leiden.

#### Superfamily CHALCIDOIDEA

This superfamily of parasitic Hymenoptera has found a number of prolific workers during the last decennia. Especially from the groups that interest us as parasites of apple leafrollers, there exist some modern taxonomic revisions.

Only one species, *Colpoclypeus florus*, is of real importance in respect to apple leafrollers; the others were only reared in small numbers. Thus we will not treat them in detail and, as far as their identity is involved, refer to the revisions.

#### Family PTEROMALIDAE

##### **Habrocytus chrysos** (Walker) (fig. 101)

This species has been dealt with by Graham (1969). We reared only three specimens as hyperparasites of the caterpillars of *Adoxophyes orana* through *Scambus brevicornis*, *Oncophanes minutus* and an unidentified Ichneumonid, respectively. Graham mentions some more hosts, so that *H. chrysos* must be considered a widely specialized hyperparasite of various Lepidoptera, through various species of parasitic Hymenoptera as direct hosts.

Adults: 28 September.

##### **Habrocytus semotus** (Walker)

We reared this species three times from apple leafrollers, namely once as a hyperparasite of *Archips podana* through *Scambus brevicornis* and two times from pupae of *Adoxophyes orana*, possibly as hyperparasites.

Graham (1969) mentions the parasite both as a primary and as a secondary parasite of various Lepidoptera, but also from certain Coleoptera and in one case from Hymenoptera Diprionidae.

Adults: 25 August—25 September.

##### **Dibrachys cavus** (Walker)

(figs. 97, 102)

According to Graham (1969) the species of *Dibrachys* have not yet been fully sorted out. On the authority of Peck (1963) he mentions *Dibrachys cavus* to be a very polyphagous parasite, usually hyperparasitic.

We reared only two small specimens from cocoons of *Apanteles ater*, parasitizing a caterpillar of *Pandemis* sp. and two specimens from a cocoon of *Diadegma* sp., *Archips podana* being the host.

Adults: 6 July.

#### Family EULOPHIDAE

##### **Pnigalio pectinicornis** (Linnaeus)

We reared only two specimens of this species, the hosts being caterpillars of *Adoxophyes orana* and *Rhopobota naevana*, respectively. Askew (1968) mentions it as a parasite of Microlepidoptera, especially of *Lithocolletis* (= *Phyllonorycter*), which are leafminers.

Adults: 4 September.

##### **Sympiesis xanthostoma** (Nees)

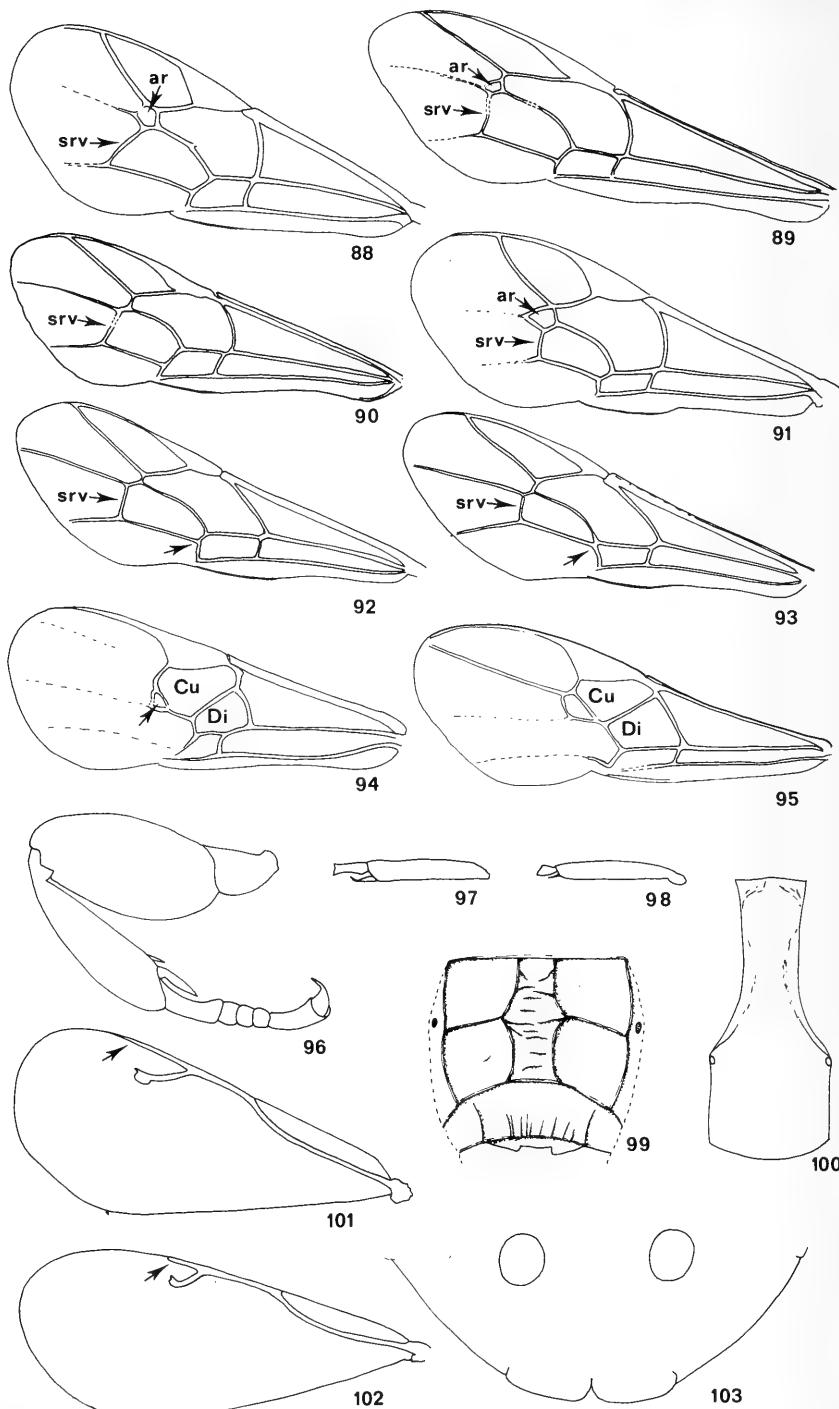
We reared two specimens, both from caterpillars of *Adoxophyes orana*. Askew (1968) mentions it a quite common parasite, especially of Tortricidae and Gracilariidae.

Adults: 30 August and 4 October.

##### **Colpoclypeus florus** (Walker)

(figs. 98, 103)

This is no doubt the most important parasite of *Adoxophyes orana* in apple orchards. We reared it in large numbers in some orchards during late summer and early autumn. There seems to be a serious discrepancy between the phenology of the parasite and of *Adoxophyes orana*, as we were not able to recover the parasite before



Figs. 88—95. Fore wing: 88, *Lysibia nana*; 89, *Teleutaea striata*; 90, *Glypta varicoxa*; 91, *Mesochorus* sp.; 92, *Habronyx canaliculatus*; 93, *Agyron anxium*; 94, *Lissogaster* sp.; 95, *Meteorus ictericus*. Fig. 96. *Triclistus palipes*, fore leg. Figs. 97—98. Fore tibia: 97, *Dibrachys cavus*; 98, *Colpocephalus florus*. Fig. 99. *Apophua cicatricosa*, propodeum. Fig. 100. *Diadegma* sp., first tergite. Figs. 101—102. Fore wing: 101, *Habrocytus chrysos*; 102, *Dibrachys cavus*. Fig. 103. *Colpocephalus florus*, front margin of clypeus.

July (Evenhuis, 1974b). During and after this month its population increases rapidly. The discrepancy makes the feasibility of the parasite in integrated control doubtful. In spite of efforts in later years, we could not find any alternative leafroller host on which it could maintain itself and reproduce, neither in apple orchards, nor outside on other foodplants than apple. Thus the problem remains unsolved. More knowledge of the bionomics and ecological particularities of the parasite seems a prerequisite in using it in integrated control in apple growing.

Adults: From the end of July until October.

It is interesting that in Swiss material, kindly sent to us by Dr. A. Schmid, Nyon, Switzerland, four additional species of parasitic Hymenoptera, reared from apple leafrollers, but only in small numbers, are represented: *Sympiesis acalle* (Walker) from *Adoxophyes orana*, *Dicladocerus westwoodii* Westwood from *Archips* sp., *Euderus albitalaris* Zetterstedt, and *Goniozus claripennis* Förster, both from *Adoxophyes orana*. The three former species are Chalcidoidea Eulophidae, the latter belongs to the Bethylidae.

#### KEY TO THE ADULT PARASITES OF APPLE LEAFROLLERS IN THE NETHERLANDS

The characters used in this key are simple. Differences between the taxa only refer to species that are dealt with in the body of the paper. Where species identification is very doubtful, the key generally does not run to species level, especially when the species are no important apple leafroller parasites.

1. Fore wings with longitudinal veins and cross veins, delimiting several cells (cf. figs. 88—95); (Ichneumonoidea) ..... 2
- Venation of fore wing strongly reduced (figs. 101, 102). Small species with metallic green or blue body; (Chalcidoidea) ..... 44
2. Second recurrent vein present (figs. 88—93: srv); first cubital cell and discoidal cell fused (figs. 88—93). Second and third gaster segments separated (cf. figs. 3, 14, 15, 34, 36); (Ichneumonidae) ..... 3
- Second recurrent vein lacking; first cubital cell (Cu) and discoidal cell (Di) separated by a vein (figs. 94, 95). Second and third gaster segments fused (cf. figs. 62, 63, 65, 66, 75, 78, 87); suture, however, generally visible; (Braconidae) ..... 25
3. Gaster depressed, petiole broadly attached

- to propodeum (cf. figs. 14, 15) ..... 4
- Gaster compressed, petiole proximally slender (cf. figs. 30, 32, 100) ..... 18
- 4. Tergites 2, 3 and 4 with oblique furrows (cf. figs. 14, 15) ..... 5
- Tergites 2, 3 and 4 without furrows (cf. figs. 3, 34, 36) ..... 9
- 5. Arolet present (fig. 89: ar). Species grey-coloured black and yellow ..... *Teleutaea striata*
- Arolet absent (fig. 90). Yellow markings less conspicuous ..... 6
- 6. Frontal tibial spur reaching to middle of first tarsal segment or beyond (fig. 19) ..... 7
- Frontal tibial spur not reaching to middle of first tarsal segment (figs. 23, 27). Genal carina not strongly sinuated (fig. 25) ..... *Glypta varicoxa*
- 7. Genal carina strongly sinuated (fig. 21); clypeus with small incision (fig. 20) ..... *Glypta nigrina*
- Genal carina moderately sinuated (fig. 17); clypeus without incision (fig. 16) ..... 8
- 8. Propodeal carinae strongly developed (fig. 99) ..... *Apophua cicatrica*
- Propodeal carinae more or less obliterated .. *Apophua* sp.
- 9. Clypeus and face conspicuously strongly convex (figs. 33, 35). Legs, especially femora, conspicuously stout (fig. 96) ..... 10
- Clypeus and face not convex. Legs rather slender ..... 12
- 10. Antennal sockets separated by a high lamella, the latter with a deep median groove dorsally, just below ocellus ..... 11
- Antennal sockets not separated by a lamella ..... *Exochus* spp.
- 11. Tergites almost completely pubescent (fig. 36) ..... *Triclistus globulipes*
- Tergites almost completely glabrous. (fig. 34) ..... *Triclistus pallipes*
- 12. Inner orbits at the level of the antennal sockets deeply incised (figs. 5, 7, 8) ..... 13
- Inner orbits not or weakly incised (fig. 1) ..... 15
- 13. Head of male with yellow markings. Ovipositor curved downwards (fig. 9) ..... *Apechthis* spp.
- Head of male black. Ovipositor straight (fig. 4) ..... 14
- 14. Head beneath antennae and centre of mesoscutum finely punctate (fig. 5). Tergites wholly black ..... *Itoplectis alternans*
- Head beneath antennae and centre of mesoscutum roughly punctate (fig. 7). Hind bor-

- der of tergites brownish ..... *Itoplectis maculator*
15. Clypeus incised (fig. 1). Tergites roughly punctate except for narrow hind strip which is finely transversely striated (fig. 3) ..... *Scambus brevicornis*
- Clypeus not incised. Tergites not roughly punctate ..... 16
16. Arolet more or less regularly pentagonal, sometimes outer crossvein lacking (fig. 88) ..... *Cryptinae*
- Arolet not pentagonal ..... 17
17. Claws pectinate (fig. 10). Scutellum, postscutellum and propodeum with yellow markings ..... *Phytodietus segmentator*
- Claws simple. Scutellum, postscutellum and propodeum entirely black ..... *Lissonota complicator*
18. Arolet large, rhombical (fig. 91) ..... *Mesochorus* sp.
- Arolet small or absent ..... 19
19. Body conspicuously slender. First gaster segment long and narrow, but not petiolated anteriorly, following segments strongly compressed ..... 20
- Body not conspicuously slender. First gaster segment petiolated anteriorly (fig. 100), following segments compressed ..... 21
20. Postnervulus intercepted near or below middle (fig. 92: arrow) ..... *Habronyx canaliculatus*
- Postnervulus intercepted distinctly above middle (fig. 93: arrow) ... *Agrypon anxiun*
21. Pronotum moderately to strongly striated; central part of propodeum excavated and transversely striated ..... *Camplex* spp.
- Pronotum rather smooth or punctate; central part of propodeum flattened or a little convex ..... 22
22. Hind tibia light brown, just like most of the legs ..... 23
- Hind tibia whitish, with dark ring proximally and distally ..... 24
23. Arolet present ..... *Tranosema arenicola*
- Arolet absent ..... *Diadegma apostata*
24. Second tergite about as long as wide ..... *Diadegma praerogator*
- Second tergite much longer than wide ..... *Diadegma fenestralis*
25. Gaster segments fused into a carapace without sutures, oval, roughly sculptured ... 26
- Only second and third gaster segments fused, sutures visible (figs. 62, 63, 65, 66, 75, 78) ..... 27
26. Clypeus with two small incisions (fig. 70). Hind border of propodeum with two lateral spinal processes only (fig. 72). Legs largely rufous ..... *Ascogaster rufidens*
- Clypeus entire (fig. 67). Hind border of propodeum except for lateral spines also with two medial spinal processes (fig. 69) ... *Ascogaster quadridentata*
27. Radial cell distinctly defined and narrow (fig. 64) ..... 28
- Radial cell not narrow ..... 29
28. First and second tergites longitudinally striated, in the female also third tergite partially striated (figs. 65, 66) ... *Agathis rufipes*
- Only first tergite longitudinally striated (figs. 62, 63) ..... *Agathis dimidiator*
29. Some veins, e.g. radial vein, pale and hardly visible, distinctly different from the other veins (fig. 46) ..... 30
- At least radial vein well-developed ..... 37
30. Second cubital cell present, small (fig. 94) ... *Lissogaster* spp.
- Second cubital cell absent (fig. 46) ..... 31
31. Pterostigma hyaline (figs. 46, 47), borders slightly darkened ..... 32
- Pterostigma dark, sometimes with light basal spot (figs. 48—52) ..... 33
32. Pronotal groove deep and crenulated over its whole length (fig. 39); propodeum with two carinae, constituting a V, space between rather smooth (fig. 53). First tergite narrowed apically ..... *Apanteles ater*
- Pronotal groove superficial, slightly crenulated in caudal half (fig. 40); propodeum with median, longitudinal, rather roughly sculptured trough (fig. 54). Side borders of first tergite more or less parallel ..... *Apanteles xanthostigma*
33. Pterostigma with light proximal spot (figs. 49, 51) ..... 34
- Pterostigma without light proximal spot (figs. 48, 50, 52) ..... 35
34. Propodeum strongly punctate reticulate (fig. 58) ..... *Dolichogenidea dilecta*
- Propodeum smooth (fig. 56) ..... *Dolichogenidea laevigata*
35. Middle hind part of propodeum excavated, crenulated in its caudal end (figs. 57, 59) ... 36
- Propodeum almost entirely smooth, with a few superficial wrinkles in the middle hind part (fig. 55) ..... *Dolichogenidea sicaria*
36. Rim near hind side of pronotum distinct (fig. 45). Pterostigma entirely dark (fig. 52) ..... *Dolichogenidea longicaudus*
- Pronotal rim only superficial (fig. 43).

- Centre of pterostigma somewhat lighter (fig. 50) ..... *Dolichogenidea corvina*
37. Second tergite at least as long as wide ..... 38
- Second tergite distinctly wider than long ..... 41
38. Mesoscutum divided into three vaulted lobes, the middle the highest (fig. 83) ..... 39
- Mesoscutum more or less flat, not divided ..... *Charmon cruentatus*
39. Pterostigma almost colourless (fig. 84) ..... *Macrocentrus thoracicus*
- Pterostigma dark, proximally somewhat lighter ..... 40
40. Body predominantly rufous ..... *Macrocentrus linearis*
- Body predominantly black ..... *Macrocentrus pallipes*
41. First gastral segment narrow proximally, with two deep pits (dorsope) in front of the middle (fig. 75) ..... *Meteorus ictericus*
- First gastral segment broadly inserted to propodeum, without deep dorsope (fig. 78) ..... 42
42. Propodeum with delimited areas, separated by irregular carinae (fig. 77) ..... *Oncophanes minutus*
- Propodeum without delimited areas (fig. 80) ..... 43
43. Mesoscutum densely pilose (fig. 79) ..... *Bracon* sp.
- Mesoscutum less pilose, hind part almost bare ..... *Bracon obscurator*
44. Fore tibiae with large, curved spur (fig. 97) ..... 45
- Fore tibiae with short, straight spur (fig. 98) ..... 46
45. Postmarginal vein as long as stigmal vein (fig. 102: arrow) ..... *Dibrachys cavus*
- Postmarginal vein longer than stigmal vein (fig. 101: arrow) ..... *Habrocytus* spp.
46. Anterior margin of clypeus medially narrowly incised (fig. 103) ..... *Colpoclypeus florus*
- Clypeus not incised ..... 47
47. Propodeum with carinae ..... *Pnigalio pectinicornis*
- Propodeum without carinae ..... *Sympiesis xanthostoma*

#### DISCUSSION

Among the Hymenopterous parasites, associated with apple leafrollers, some species were reared commonly and in rather large numbers, whereas most of them were only obtained occasionally. Many of these latter are no rare species

whatever, but do not really belong to the apple orchard community (table 1).

In provisional investigations parasites were also reared by collecting leafroller caterpillars on other foodplants and in different habitats. Many of these parasites belong to other species than those from apple orchards or to the same species but in entirely different ratios. The same feature holds also for some leafroller species, e.g., *Adoxophyes orana* was only found occasionally outside apple orchards. If these investigations might prove to have a general bearing, it could mean that leafroller caterpillars in habitats adjoining apple orchards, only play a minor role as a reservoir for apple leafroller parasites. It must be born in mind that there are several types of apple orchards, with different ecological conditions to satisfy the needs of the several parasite species. As an example of the special needs of a leafroller parasite might be mentioned Zwölfer's remark concerning *Apanteles xanthostigma*, the female of which only looks for its hosts in the shrubs and the lowermost parts of the trees (Zwölfer, 1962). Such ecological preferences might at least partly explain the scarcity in apple orchards of so many parasite species that are quite common elsewhere.

It is obvious that numerous investigations are still necessary for obtaining a more clear insight in the intricate interrelationships between the different leafroller species on apple and their parasites. By rearing parasites from known hosts, large series of parasites belonging to one species, may be obtained. Rearing not only gives information about host specificity of the parasite, but also may be of interest in understanding species variation.

It does not seem superfluous to emphasize the tremendous importance of a sound taxonomical base in distinguishing the species. From our investigations it may be concluded that for most groups of Hymenopterous leafroller parasites this base is not present and this might apply as well to the group of parasitic Hymenoptera as a whole.

Parasitic Hymenoptera constitute an insect group very rich in species. We estimate that Dutch species far outnumber 7000, the total number of insect species in the Netherlands probably not exceeding 25,000. We do not venture to give figures for larger areas, but we suppose that parasitic Hymenoptera are extraordinary numerous throughout the world. Large genera with quite similar species are no excep-

Table 1. Enumeration of parasitic Hymenoptera with the numbers that were reared from their apple leafroller hosts.

	<i>Pandemis cerasana</i>	<i>Pandemis heparana</i>	<i>Archips rosana</i>	<i>Archips podana</i>	<i>Archips xylosteana</i>	<i>Clepsis spectrana</i>	<i>Addoxophyes orana</i>	<i>Ptycholoma lecheana</i>	<i>Acleris spp./Crocis pomifolia</i>	<i>Spilonota ocellana</i>	<i>Rhopobota naevana</i>	<i>Hedya nubiferana</i>	Host unknown
<i>Scambus brevicornis</i>	1						87						7
<i>Itolectis alternans</i>	2	1	2				29	2		1			11
<i>Itolectis maculator</i>	1	4					3					3	1
<i>Apechthis compuncutor</i>													1
<i>Apechthis quadridentatus</i>	1												
<i>Apechthis rufatus</i>		1						1					
<i>Phytodietus segmentator</i>		6	5										
<i>Gelis</i> spp.		2					1			1			
<i>Acrolyta</i> sp.										1			
<i>Lysibia nana</i>		3											
<i>Teleutaea striata</i>	1	3					65	7					2
<i>Apophua cicatricosa</i>	1	6											
<i>Apophua</i> sp.					1								
<i>Glypta nigrina</i>							2	2					
<i>Glypta varicoxa</i>									20				
<i>Lissonota complicator</i>				22									4
<i>Diadegma praeorgator</i>	2	4	5	1			19	9	2	9		7	2
<i>Diadegma apostata</i>							1					1	
<i>Diadegma fenestralis</i>				1									
<i>Tranosema arenicola</i>	1	6	22	2			1			3			2
<i>Campoplex difformis</i>	1						1		3				
<i>Campoplex</i> sp.									5				1
<i>Campoplex</i> spp.		2		4			2	2	3				
<i>Mesochorus silvarum</i>	1						1						
<i>Stictopishus lineatus</i>							1						1
<i>Triclistus pallipes</i>										10			
<i>Triclistus globulipes</i>					2	1							
<i>Exochus</i> sp. 1									1				
<i>Exochus</i> sp. 2							1						
<i>Habronyx canaliculatus</i>					2								
<i>Agrypon anxiun</i>									3	1			
<i>Apanteles ater</i>		24		43			12	2	6				8
<i>Apanteles xanthostigma</i>	26	8					38	2		14		12	7
<i>Dolichogenidea laevigata</i>									1				
<i>Dolichogenidea dilecta</i>													1
<i>Dolichogenidea longicaudus</i>										1		2	
<i>Dolichogenidea corvina</i>								1		1			1
<i>Dolichogenidea sicaria</i>				1				1		1		1	
<i>Lissogaster</i> spp.	1	6					1		2				2
<i>Agathis dimidiator</i>										27			
<i>Agathis rufipes</i>										30			2
<i>Ascogaster quadridentata</i>										24		5	5
<i>Ascogaster rufidens</i>	13	28	1				6						3
<i>Meteorus ictericus</i>	2	6	4	4			24			19	1		12
<i>Oncophanes minutus</i>		1					10						
<i>Bracon</i> sp.							1						
<i>Bracon obscurator</i>										1			
<i>Macrocentrus linearis</i>	13	113		19									1
<i>Macrocentrus pallipes</i>												1	
<i>Macrocentrus thoracicus</i>													
<i>Charmon cruentatus</i>									1				
<i>Habrocytus chrysos</i>							3						
<i>Habrocytus semotus</i>						1		2					
<i>Dibrachys cavus</i>	1		1										1
<i>Pnigalo pectinicornis</i>								1					
<i>Sympiesis xanthostoma</i>								2					
<i>Colpocephalus florus</i>	3						248						3

tion in this group. Thus it is hardly surprising that identification meets with very large difficulties. Yet, exact species discrimination seems essential, as very similar species show considerable differences in biological and ecological respects.

Descriptions of species by the earlier taxonomists are generally too poor to allow of any conclusion about their identity. They often suit more than one species. Later authors, who tried to interpret them in their own way, added new species, just as ill-described. In this way taxonomic literature has been overburdened with "species" from which no one can establish their identity to-day.

In the past a number of taxonomic works have been written, dealing with larger groups of parasitic Hymenoptera and based mainly on a compilation of these insufficiently described species, which were often not fully understood by the compilators themselves. Some examples of these works are Schmiedeknecht's *Opuscula Ichneumonologica* (1902—1936), Fahringer's *Opuscula Braconologica* (1928—1937), Kieffer's work in "Das Tierreich" on Proctotropoidea (1914—1926) and that of Dalla Torre & Kieffer on Cynipoidea (1910), also in "Das Tierreich". It is not our intention to criticize these works. They present excellent surveys of the knowledge of the several species at that time, and any specialist who occupies himself with these groups now, has to consult them. However, they do not satisfy the needs of a modern entomologist who wants to know the reliable names and taxonomical status of the species which he encounters in his ecological investigations. Unreliable species names of parasitic Hymenoptera show up in reviewing journals, e.g., The Review of Applied Entomology, and from these they are compiled in comprehensive works like Thompson's host-parasite lists.

In view of the difficulties discussed above, it cannot be expected that the gap in our taxonomic knowledge of the species of parasitic Hymenoptera will be filled up within a reasonable time. Fortunately in the last decades an increasing interest in the taxonomy of parasitic Hymenoptera has arisen, and many groups have now been or will soon be revised.

Ecologists have to rely on identifications by specialists. Only these specialists are thoroughly acquainted with the taxonomic difficulties and their nomenclatorial consequences. Only a spe-

cialist in a certain not too large taxonomic group can really judge in how far his identifications are reliable.

It might be desirable that a specialist, in identifying material on behalf of ecological investigations, should add some more information than merely the name. The ecologist should also be informed about the reliability of the species name, which can only be judged by the specialist.

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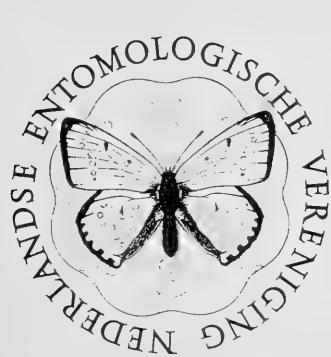




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# ON THE SPECIES OF THE POLYGONUS GROUP OF PROGOMPHUS WITH A DESCRIPTION OF A NEW SPECIES (ODONATA, GOMPHIDAE)

by

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## ABSTRACT

*P. occidentalis* spec. nov. (♂ holotype: San Antonio, Venezuela?) is described and elucidated by figures. The right pair of wings of *P. polygonus* Selys is depicted. A distribution map of *P. phyllochromus* Ris is given. The male of *P. abbreviatus* Belle is redescribed and its female is described for the first time. The four species mentioned here are forming an infragenetic group.

## INTRODUCTION

Since my revision of the genus *Progomphus* Selys in 1973, five new species have been described, two from Brazil (*P. victor* St. Quentin, 1973, and *P. perithemoides* Belle, 1980), one from Paraguay (*P. flinti* Belle, 1975), one from the USA (*P. bellei* Knopf & Tennesen, 1980) and one from Venezuela (*P. racenisi* De Marmels, 1983). In the present account a new species, *P. occidentalis*, is described from continental South America. The new descriptions show that the genus *Progomphus* is very rich in species, and that we still have not come to the end of our discoveries.

Together with *P. polygonus* Selys, *P. phyllochromus* Ris and *P. abbreviatus* Belle, the new species mentioned above belongs to an infragenetic group, the *polygonus* group. The members of this group correspond in the occurrence of an extra cubito-anal cross-vein in the wings (occasionally present in *P. abbreviatus*), the more or less broken distal side of the fore wing discoidal triangle, the medially excised posterior margin of the occipital plate, the wedge-shaped first pale antehumeral stripes, and the lack of a second pale antehumeral stripe immediately in front of the humeral sutures, while the abdomen of the females is about as long as the hind wings.

The new material of the *polygonus* group enables me to publish additional data on its known members. A figure of the right pair of wings of the female lectotype of *P. polygonus* is given. A distribution map of *P. phyllochromus* has been made with the aid of old and new records. The male of *P. abbreviatus*, known only from a sin-

gle male in poor condition, is redescribed from fully mature specimens; and the female of this species is described for the first time.

The material on which the present paper is based belongs to the institutions and personal collections mentioned below; the names are preceded by the abbreviations used throughout the text and followed by the names of the persons from whom material was received on loan or as a gift. These persons are most gratefully acknowledged here.

- ANSP — Academy of Natural Sciences of Philadelphia, Philadelphia; Dr. Dave Rentz.  
FSC — Florida State Collection of Arthropods, Gainesville; Prof. Dr. Minter J. Westfall, Jr.  
IML — Instituto Miguel Lillo, San Miguel de Tucumán; Dr. A. Willink.  
IRSN — Institut Royal des Sciences Naturelles de Belgique, Bruxelles; Dr. Georges Demoulin.  
IZM — Instituto de Zoología Agrícola, Maracay; Dr. F. Fernández Yépez and Mr. Jorge de Marmels.  
ML — Rijksmuseum van Natuurlijke Historie, Leiden; Dr. P. H. van Doesburg.  
MP — Muséum National d'Histoire Naturelle, Paris; Dr. Jean Legrand.  
SMF — Natur-Museum Senckenberg, Frankfurt am Main; Dr. Heinz Schröder.

**Progomphus polygonus** Selys, 1878  
(fig. 23)

This species was described after two very teneral females from Merida, Venezuela. No additional material is available. In 1973 a lectotype was designated by me. In the present paper a depiction of the right pair of wings of the lectotype is published.

*P. polygonus* is the largest representative of the *polygonus* group. The reticulation of its wings is denser than that of the other members. The trigonal interspace in the fore wings of the lectotype starts with three rows of cells from the triangle outwards, three cells long. The distance between the nodus and the pterostigma is a little more than 2.75 times the length of the pterostigma. The abdomen of the female is relatively shorter than that of the females of the other members of the group. But the two females of *P. polygonus* are very teneral and fully mature females may have a relatively longer abdomen.

**Progomphus phyllochromus** Ris, 1918  
(figs. 1—4, 6)

Material. — Argentina: Catamarca, Concepción, 15.i.1960, 1 ♂, 1 ♀, FSC; Salta, Orén (24 km of Agua Blancos), 9.v.1969, 1 ♂, IML, all A. Willink leg. — Colombia: 1 ♀ (ex coll. R. Martin), MP. — Venezuela: Aragua, Cumbre de Choroní, 13.viii.1957, 1 ♀ (author's collection), 1 ♀, J. Rácenis leg.; Miranda, Petare, 26.xi.1961, 1 ♂, Bordon leg., IZM.

This mountain species is chiefly Andean in its distribution and it occurs from the north coast of Venezuela to Catamarca in Argentina (distance between the two localities almost 6000 km). It has been recorded from Argentina, Bolivia, Colombia, Ecuador, Peru and Venezuela. In drawing up the distribution map (fig. 6) the present localities as well as those published earlier (Ris, 1918; Belle, 1973) were used.

The male from Salta is small and its wings have a less dense reticulation. The measurements are: total length, 35.5 mm; abdomen, 26 mm; hind wing, 23 mm; costal edge of pterostigma in fore wing, 3.3 mm. The fore wings have an open subtriangle, a single row of cells in the anal field, and no extra cubito-anal cross-vein. The frons is higher than is normally the case, and there is a weak development of a frontal ridge. The two wedge-shaped, (first) pale antehumeral stripes are rather narrow and they are almost parallel-sided on the dorsal half.

The female from Colombia has no extra cubito-anal cross-vein in the wings.

The larva of *Progomphus*, described by Needham (1941) as No. 14, most likely belongs to *P. phyllochromus*. The venational characters found in the pair of wings of this larva are in agreement with those of the adults of *P. phyllochromus*, and its place of capture (Estado Miranda) lies within the range of the species. Needham's larva No. 14 differs from that of *P. abbreviatus* described by De Marmels (1981b) in having the front margin of the middle lobe of the labium armed with a single median tooth instead of one submedian pair of such teeth (Needham, 1941: 240).

**Progomphus abbreviatus** Belle, 1973  
(figs. 7—17)

Material. — Colombia: Dept. Magdalena; Sierra San Lorenzo (4500–5600 ft), Hacienda Cincinati, 20.vii.1920, 1 ♂, ANSP; Prima, 1.vi.1965, 1 ♂, J. & B. Bechyne leg., IZM; Sierra de Perija (1350), Mission Finca Marganta (6 km SW of Socorpa, rocky stream, half shaded), 7—8.viii.1968, 1 ♂, Borys Malkin leg., ML. — Ecuador: 1 ♂, MP. — Venezuela: Miranda, Sebucán, 16.x.1955, 3 ♂ (author's collection), 3 ♂ all Klisans leg.; Miranda, El Marqués, Quebrada Pasaquire, Avila (1000 m), 10.x.1980, 1 ♀, J. de Marmels leg., IZM.

This species was described after a single male from Colombia. The type is in poor condition, very teneral and flattened for its entire length. Due to this bad condition some features are misinterpreted or insufficiently described in the original description. Therefore descriptive notes of the present fully mature males are given below.

The female is also described.

Male. — Total length, 39—41 mm; abdomen, 29.5—30.5 (incl. app.); hind wing, 23—25.5 mm; costal edge of pterostigma in fore wing, 3.0—3.5 mm.

Labrum with grey-green band along free border, the width of the band very narrow in one male but very broad in another male. Anteclypeus, lateral sides of postclypeus and bases of mandibles externally grey-green. Frons low, without anterior ridge, its superior surface largely grey-green but dark brown at base. Vertex and occipital plate dark brown. Postocellar ridges well-developed. Mid-dorsal width of oc-

cipital plate a quarter the length of frontal margin of occipital plate. Posterior margin of occipital plate concave and with a shallow median excision which is very small and V-shaped in some males. Crest of occiput with very long brown hairs. Rear of head brown but tempora with a pale green spot and a (lower) pale green band. Labrum and adjacent mouth parts pale green.

Prothorax dark brown, the hind lobe blackish brown. Dark colour of pterothorax blackish brown. Pale antehumeral stripes grey-green, very broad in male from Ecuador. Three pale lateral stripes of pterothorax olive-green.

Legs brown but inner sides of femora green. Third tarsi three-quarters the length of third tibia.

Abdomen dark brown, becoming blackish brown on apical segments. Sides of 1 entirely green. Sides of 2 largely green. Genital hamules and hood of penial peduncle brown. Sides of 3 with a long, triangular, green basal spot. Segments 2 to 7 with a pale mid-dorsal line which is rather wide and green on 2, narrow but green at base and becoming yellow at apex on 3, very fine and yellow on 4 to 7. Dorsum of 7 yellow on basal third. Caudal appendages black but upper surface of superiors pale on apical two-fifths. Inner process of branches of inferior appendage variable, generally reduced to a low hump but in some males entirely lacking; length of branch beyond this inner process (if available) also variable.

Venetion of wings dark brown but costa with a very fine and inconspicuous yellow line. Pterostigma yellowish brown. Two cubito-anal cross-veins in addition to inner side of subtriangle in seven fore wings; other wings without extra cubito-anal cross-veins. Discoidal triangle open in one fore wing, two-celled in other wings. Subtriangle three-celled in two fore wings and two hind wings, two-celled in other wings. Supratriangle (once) crossed in two hind wings, open in other wings. Trigonal interspaces in fore wings starting with two rows of cells from triangle outwards, those in hind wings starting with a row of two (one male) or three (other males) cells against triangle followed by two rows of cells. Anal field in five fore wings one cell wide, in other fore wings two cells wide. Second anal interspace in three hind wings starting with a single large cell against anal vein, in other hind wings with two cells against anal vein.

Female (hitherto unknown; degutted and treated with acetone). — Total length, 37.5 mm;

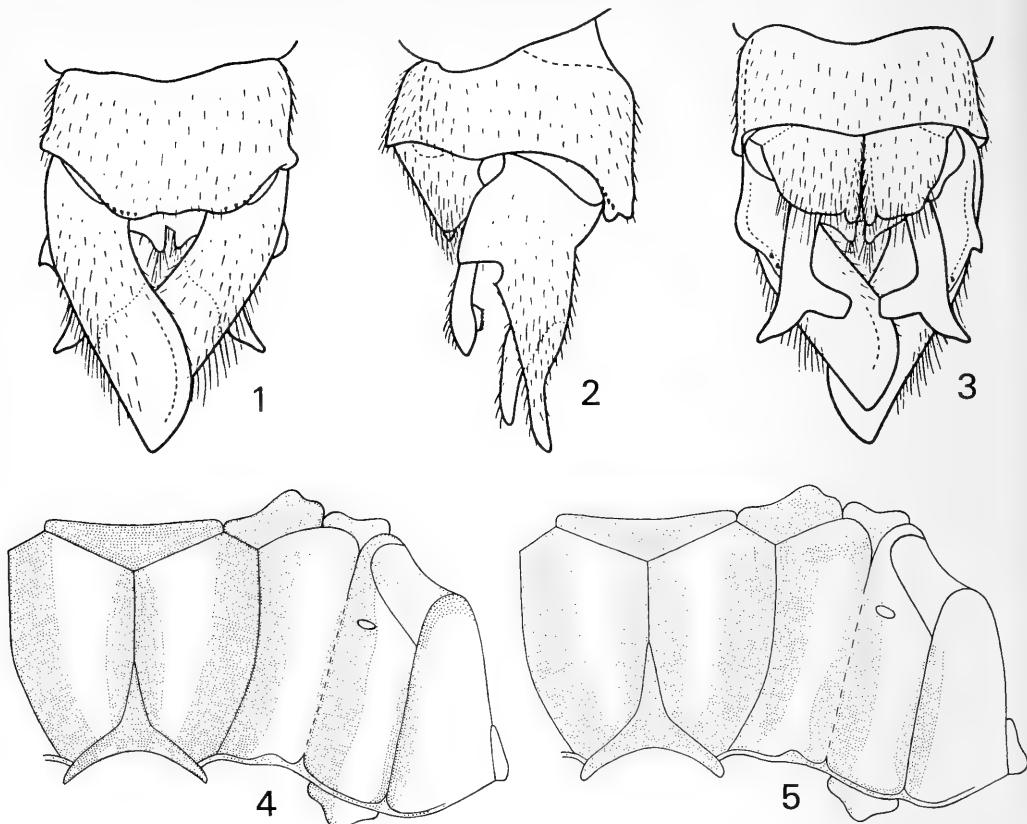
abdomen, 28 mm (incl. app.); hind wing, 26.5 mm; greatest width of hind wing, 8.2 mm; costal edge of pterostigma in fore wing, 3.7 mm.

Similar to male regarding stature and colour design but abdomen stouter. Grey-green anterior band on superior surface of frons narrower than in male, in dorsal view occupying one-third of superior surface of frons. Pale markings on pterothorax greenish white, on abdomen yellowish white. Second pale antehumeral stripes somewhat narrower than in male. Pale markings on abdomen as follows: A fine mid-dorsal line on 2 to 8; lateral stripes becoming successively shorter on 4 to 6, reaching to apex of segment on 2 and 3, and to a point half way the segment on 6, the stripes being interrupted by the supplementary transverse carinae; dorsum of 7 pale from base to supplementary transverse carinae. Abdominal segments 7, 8, 9, and 10 approximately in ratio 46 : 26 : 19 : 10, with the caudal appendages (stylets) 15 on the same scale. Vulvar lamina one-third the length of ninth sternum, its posterior margin medially excised U-shaped for three-quarters the length of vulvar lamina. Caudal appendages white at tips and spine-like pointed.

Basal subcostal cross-vein present. No extra cubito-anal cross-vein. Anal field in fore wings two cells wide. Nodal index 14 : 17—18 : 12/13 : 13—14 : 13. Second primary antenodal cross-vein the sixth in right fore wing, the fifth in other wings. Intermedian cross-veins 6—6/4—4 in fore and hind wings, respectively. Supratriangles open. Subtriangle in right fore wing two-celled, in other wings three-celled. Discoidal triangles two-celled. Trigonal interspaces starting with two (right fore wing) or three (other wings) cells against triangle followed by two rows of cells. Hind wings with five paranal cells, four (left) and five (right) postanal cells, and four to five rows of cells posterior to Cu2.

The female of *P. abbreviatus* resembles that of *P. phyllochromus* but the latter has the frons distinctly angled, the occipital plate much broader (mid-dorsal width two-fifths the length of frontal margin), and the fore wings generally with extra cubito-anal cross-veins.

Mr. De Marmels wrote me that several more females were seen and photographed at the place where the female described was captured (cf. De Marmels, 1981a: 40). The following venational characters could be determined from the colour slides: ♀ (1—15.viii.1979), number of antenodal cross-veins in left fore wing 16 and



Figs. 1—4. *Progomphus phyllochromus* Ris, ♂ holotype: 1, tenth abdominal segment and caudal appendages, dorsal view; 2, the same, left lateral view; 3, the same, ventral view; 4, diagram of thoracic colour pattern. Fig. 5. *Progomphus occidentalis* spec. nov., ♂ holotype: Diagram of thoracic colour pattern.

in left hind wing 12, discoidal triangles and subtriangles in left wings two-celled; ♀ (viii-ix. 1979), nodal index of left pair of wings 11 : 14/12 : 11. A female collected by him at the same place on 25.ix.1981 has the following features: total length, 37.5 mm; abdomen, 27.5 mm; hind wing, 25 mm; costal edge of pterostigma in fore wing, 3.8 mm. Sternum of abdominal segment 10 not shorter than sternum of abdominal segment 9. All triangles and subtriangles two-celled. Trigonal interspace starting with two cells against triangle in fore wings, with three cells in hind wings. Nodal index 11 : 16—17 : 12/11 : 12—12 : 12. Second primary antenodal cross-vein the fifth in all wings (all data communicated by Mr. De Marmels).

The larva of *P. abbreviatus* was described by De Marmels (1981b).

#### *Progomphus occidentalis* spec. nov. (figs. 5, 18—22)

Material. — Venezuela (?): San Antonio, 1 ♂ (holotype), MP.

Male (abdomen broken between segments 5 and 6). — Total length, 43 mm; abdomen, 33.5 mm; hind wing, 26.5 mm; greatest width of hind wing, 8 mm; costal edge of pterostigma of fore wing, 3.6 mm.

Face brown. Frons low and slightly angled, its superior surface with a broad, leaden-grey anterior band. Vertex dark brown, the posterior ridge of lateral ocelli swollen and provided with long brown hairs. Occipital plate dark brown, its posterior margin concave in middle portion, provided with long brown hairs. Rear of head brown above. Tempora with a brown-yellow

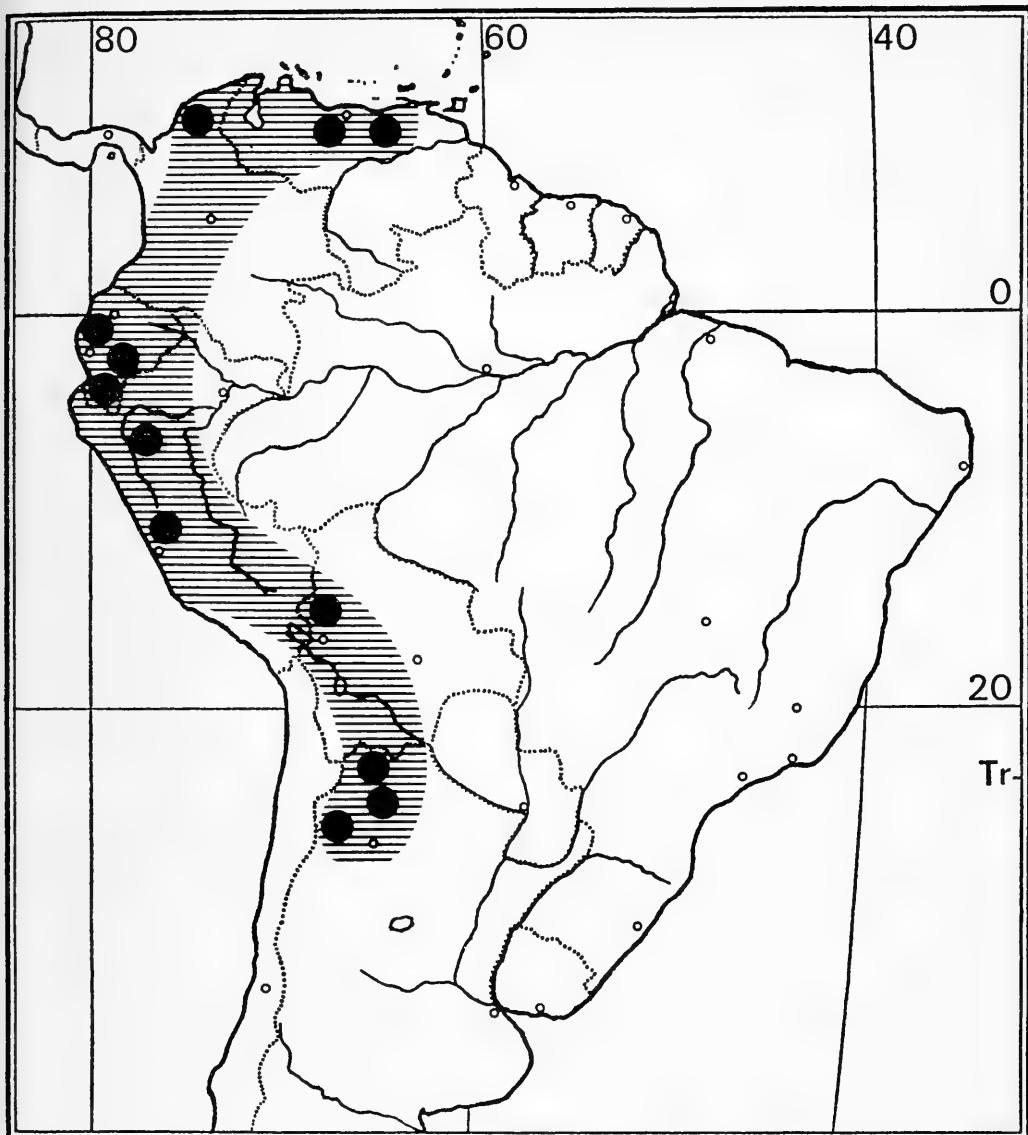


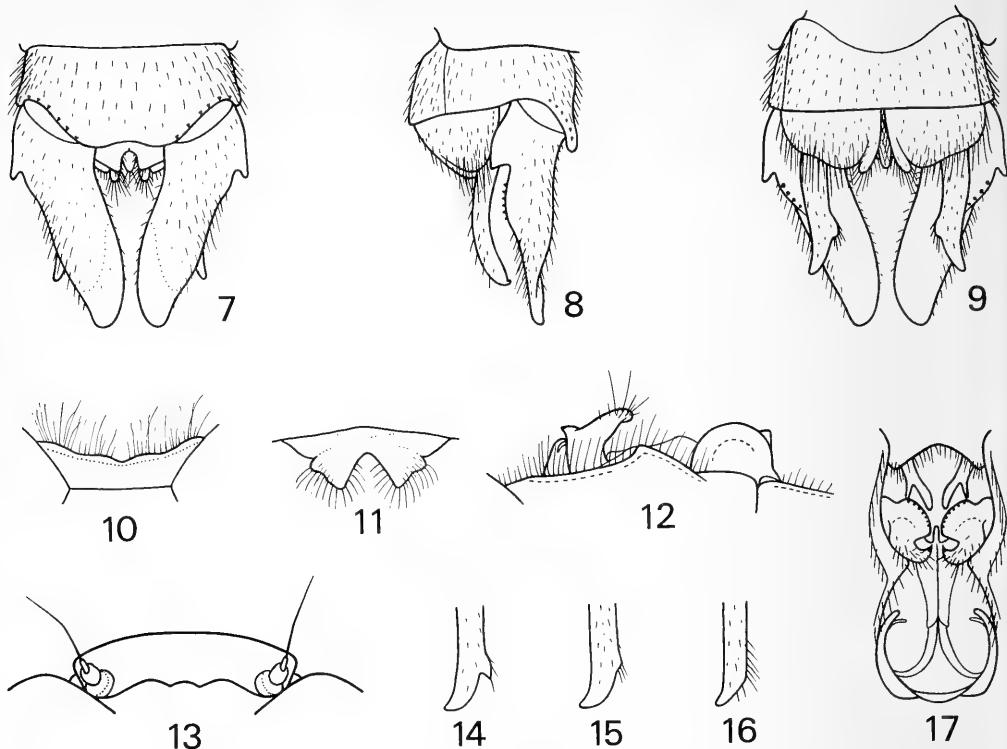
Fig. 6. Distribution of *Progomphus phyllochromus* Ris.

spot. Lower parts of rear of head brown-yellow. Labium and adjacent mouth-parts pale brown.

Prothorax dark brown. Pterothorax dark brown with green stripes, its colour design shaped as shown in diagram fig. 5.

Legs brown but inner side of first femora green. Third tibia three-quarters the length of third femur. Lamina tibialis of first tibiae one-fifth the tibial length.

Wings clear. Venation brown but frontal side of costa with a fine yellow line. Pterostigma brownish yellow, surmounting 5½–6 cells. Distance between nodus and pterostigma 2½ times the length of pterostigma. Basal subcostal cross-vein present. Nodal index 11 : 15–16 : 10/11 : 11–12 : 11. Second primary antenodal cross-vein the fifth. Intermedian cross-veins 6—5/5—5 in fore and hind wings, respectively. All supratriangles open. All subtri-



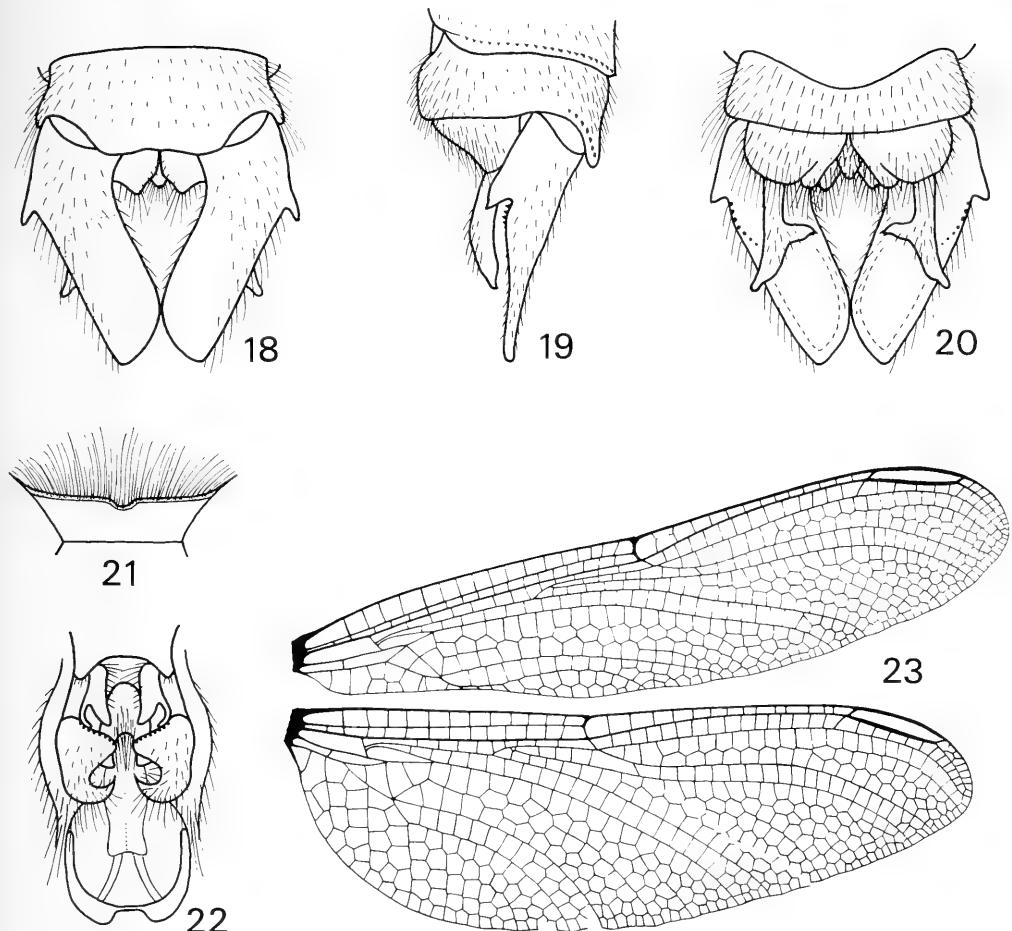
Figs. 7—17. *Progomphus abbreviatus* Belle: 7, tenth abdominal segment and caudal appendages of male, dorsal view; 8, the same, left lateral view; 9, the same, ventral view; 10, occipital plate of female; 11, vulvar lamina; 12, accessory genitalia, right lateral view; 13, frons of male, dorsal view; 14, ventral view of right branch of inferior caudal appendage, male from Miranda; 15, the same, another male from Miranda; 16, the same, male from Sierra San Lorenzo; 17, accessory genitalia, ventral view.

angles and discoidal triangles two-celled. There is an extra cubito-anal cross-vein in each wing. Trigonal interspace in fore wings starting with two rows of cells from triangle outwards (that of left fore wing with an extra initial cell next hind angle of triangle) eight cells long, in anterior row, that in hind wings starting with three rows of cells against triangle followed by two rows of cells two (right) and three (left) cells long, in anterior row. Anal field in right fore wing one cell wide, that in left fore wing with one of the cells doubled. Hind wings with five (right) and six (left) paranal cells, four rows of cells behind Cu<sub>2</sub> and a three-celled anal triangle.

Abdomen predominantly dark brown. Mid-dorsum of segments 2 to 7 with a yellow line which is rather broad on segment 2 but which becomes very fine on segments 5 to 7. Sides of segment 2 with yellow marking behind and be-

low auricle. Lower parts of sides of segments 3 to 6 with yellow marking from base to apex of segment. Basal third portion of segment 7 yellow. Caudal appendages shaped as shown in accompanying figures, blackish brown, the superiors becoming pale on apical half.

The unique (pinned) specimen of *P. occidentalis* was found in the collection of René Martin at Paris. Attached to the pin is an old label "*Progomphus polygonus* Selys S. Antonio" but there is no label referring to the country in which the locality San Antonio lies. However, from its relationship with the other members of the *polygonus* group we can say that the specimen hails from western continental South America, hence the specific name *occidentalis*. But René Martin referred the male to *P. polygonus*, a species known only from Venezuela. I therefore suspect that the specimen is from the west of



Figs. 18—22. *Progomphus occidentalis* spec. nov., ♂ holotype: 18, tenth abdominal segment and caudal appendages, dorsal view; 19, the same, left lateral view; 20, the same, ventral view; 21, occipital plate; 22, accessory genitalia, ventral view. Fig. 23. *Progomphus polygonus* Selys, ♀ lectotype: right pair of wings.

this country (State of Táchira) where a village San Antonio lies.

*P. occidentalis* is intermediate between *P. phyllochromus* and *P. abbreviatus* but it is more closely related to the first than to the second species. The males of *P. occidentalis* and *P. phyllochromus* are distinguished by the following features: (1) apex of branches (part beyond anteapical inner process) of inferior caudal appendage longer in *P. occidentalis* than in *P. phyllochromus*; (2) inner process of branches of inferior caudal appendage acute and ending in two minute teeth in *P. occidentalis*, truncated and furnished with a marginal row of minute teeth in *P. phyllochromus*; (3) lateral outer side

of superior caudal appendages between basal dilatation and proximal denticle of inferior carina not emarginated in *P. occidentalis*, widely emarginated in *P. phyllochromus*; (4) tip of posterior hamule of accessory genitalia very acutely pointed and strongly recurved in *P. occidentalis*, and longer than that in *P. phyllochromus*.

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# A REVIEW OF THE GENUS ZONOPHORA SELYS (ODONATA, GOMPHIDAE)

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## ABSTRACT

The genus *Zonophora* Selys is revised. A number of problems in the classification of its members are solved and elucidated by figures. A new subfamily, the Zonophorinae, is introduced. *Z. diversa* spec. nov. (♂ holotype: Nova Teutonia, Santa Catarina, Brazil), *Z. campanulata annulata* subspec. nov. (♂ holotype, ♀ allotype: Jataí, Goiás, Brazil) and *Z. nobilis* spec. nov. (♂ holotype: Taracua, Amazonas, Brazil) are described. *Z. machadoi* St. Quentin and *Z. obscura* Belle are considered to be subspecies of *Z. campanulata* (Burmeister) and *Z. solitaria* Rácenis, respectively. The females of these subspecies are also described. A neotype for the type-species of the genus and lectotypes for *Z. supratriangularis* Schmidt and *Z. wucherpfennigi* Schmidt are selected. Illustrations of some structures of the accessory genitalia of *Z. surinamensis* Needham are given. A key to the species and subspecies is constructed. New distributional records and distribution maps are added.

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## INTRODUCTION

The genus *Zonophora* was created for a certain Neotropical gomphid by Selys in 1854. Into this genus, he placed *Diastatomma campanulata*, described on the basis of a single male from

Brazil by Burmeister (1839). No further additions were made to the genus for fifteen years, when Selys (1869) published descriptions of two new species (*batesi* and *calippus*). Fifty-one years later, Campion (1920) described *spectabilis*. In 1941, Schmidt described two species (*supratriangularis* and *wucherpfennigi*) and one subspecies (*klugi* as subspecies of *calippus*). Needham (1944) described one species (*surinamensis*), St. Quentin (1973) one species (*machadoi*), Rácenis (1970) one species (*solitaria*), and Belle (1976) two species (*regalis* and *obscura*). One species referred to *Zonophora* (*Z. rokitanskyi* St. Quentin, 1973) does not fall within the limits of this genus and was assigned to *Diaphlebia* Selys, 1854 (Belle, 1977a). Here I report on material of two new species (*diversa* and *nobilis*) and one new subspecies (*campanulata annulata*), bringing the total number of taxa to fifteen.

Schmidt (1941) treated *spectabilis* and *klugi* as subspecies but Belle (1963) elevated them to the rank of species. A restudy of these representatives, however, has revealed that there is little reason for retaining this status and that Schmidt's classification should be followed. St. Quentin (1973) considered *wucherpfennigi* as a subspecies of *batesi* but here *wucherpfennigi* is treated as species, following again Schmidt. On the contrary, St. Quentin's *machadoi* and Belle's *obscura* are considered subspecies of

*campanulata* and *solitaria*, respectively. It is clear that in the interests of a stable nomenclature a neotype designation for the type-species of the genus is required since the holotype of Burmeister's *campanulata* must be considered lost.

The knowledge of the proventriculus of larval *Zonophora* has led to the introduction of the subfamily Zonophorinae, to contain the genus *Zonophora*. The diverse specific characters show that the members of the genus *Zonophora* can be conveniently divided into five groups. The critical structures on which the present classification is based are elucidated by original camera lucida drawings. Distributional maps for the groups are added and a key to the species and subspecies is constructed. I take the opportunity to publish illustrations of some important structures of the accessory genitalia of *Z. surinamensis*.

#### MATERIAL AND ACKNOWLEDGEMENTS

The material on which the present review is based belongs to the institutions and personal collections mentioned below; the names are preceded by the abbreviations used throughout the text of this paper.

- AC — Author's collection;
- BM — British Museum (Natural History), London; Dr. Peter H. Ward;
- CC — Collection Cook, Center; Mr. Carl Cook;
- CJ — Collection Jurzitz, Karlsruhe; Prof. Dr. Gerhard Jurzitz;
- CM — Collection Machado, Belo Horizonte; Prof. Dr. Angelo B. M. Machado
- CU — Cornell University, Ithaca; Dr. L. L. Pechuman;
- IRSN — Institut Royal des Sciences Naturelles de Belgique, Bruxelles; Dr. Georges Demoulin;
- IZM — Instituto de Zoología Agrícola, Maracay; Dr. F. Fernández Yépez;
- ML — Rijksmuseum van Natuurlijke Historie, Leiden; Dr. P. H. van Doesburg;
- MP — Muséum National d'Histoire Naturelle, Paris; Dr. Jean Legrand;
- UMMZ — Museum of Zoology, University of Michigan, Ann Arbor; Mrs. Leonora K. Gloyd and Dr. T. E. Moore;
- SMF — Natur-Museum Senckenberg,

Frankfurt-am-Main; Dr. Heinz Schröder.

For the loan of material I am also indebted to the following persons: Mr. Jorge de Marmels (Caracas) and Dr. Janis Rácenis (†) (Caracas).

#### Zonophora Selys, 1854

*Zonophora* Selys, 1854: 80 (61 sep.); 1873: 517 (73 sep.). Selys & Hagen, 1858: 493—494 (233—234 sep.). Kirby, 1890: 75. Karsch, 1890: 371. Carpenter, 1897: 453. Navás, 1916: 28. Campion, 1920: 139—140. Williamson, 1920: 9, 11—12. Kennedy, 1928: 370. Tillyard & Fraser, 1938—1940: 372. Byers, 1939: 21. Fraser, 1940: 549; 1957: 93. Needham, 1940: 388—389; 1944: 172—173, 215, 218, 221—222. Schmidt, 1941: 76—78. Belle, 1963: 60, 62—63; 1976: 197, 200, 206; 1979: 46. St. Quentin, 1967: 150; 1973: 335, 337—338, 341, 361. Paulson, 1977: 179. Kauta, 1979: 268. Davies, 1981: 33.

Type species. — The type-species of the genus *Zonophora* is *Diastatomma campanulata* Burmeister, 1839, as designated by Kirby (1890).

Position. — The systematic position of *Zonophora*, based on a certain combination of venational characters, has been changed several times. Williamson (1920) placed *Zonophora* in his "Zonophora series", a series which only contained this genus. *Zonophora* was characterized by the discoidal triangles and subtriangles of the fore and hind wings being similar, the discoidal triangles long and once crossed, the subtriangles and supratriangles all free, absence of trigonal supplements and sectors of *Rs* and *M<sub>4</sub>*, and by the nearly right proximal angle at the point of separation of *A<sub>1</sub>* from *Cu<sub>2</sub>* + *A<sub>1</sub>* and not as obtuse as the distal angle at the same point. However, the supratriangles are normally crossed in two species and incidentally crossed in some other species. In the classification as proposed by Tillyard and Fraser (1938—1940), *Zonophora* becomes one of the members of the Ictinogomphinae, distinguished by their position of crossed discoidal, supra- and subtriangles. However, *Zonophora* has the subtriangles never crossed and the supratriangles of most species generally not crossed. In the revised reclassification, Fraser (1957) transferred *Zonophora* into the Gomphoidinae, which were separated from the other genera by the presence of crossed discoidal, supra- and subtriangles, and in having only a single cross-vein (Ac) in the cubital space. *Zonophora*, however, has uncrossed subtriangles and generally uncrossed supra-

triangles while in some species there are normally two or three cubito-anal cross-veins in addition to the inner side of the subtriangle (Belle, 1963, tabs. 3, 4). Belle (1979), finally, placed *Zonophora* in the Epigomphinae, which were characterized by the uncrossed subtriangles in the fore wing, the number of intermedian cross-veins in the hind wing being two or more, and the absence of a trigonal supplement. However, the aberrant proventricular armature of larval *Zonophora* (cf. below) shows the isolated position of this genus in the Gomphidae and justifies the erection of a sixth subfamily, the Zonophorinae, to contain *Zonophora*. The proventricular character together with the venational character for the hind wings cited above (proximal angle at point of separation of A1 from Cu<sub>2</sub>+A1 nearly a right angle, and not as obtuse as distal angle at same point) separate *Zonophora* from the rest of the Epigomphinae in which it was lastly placed.

**Immature stages.** — In 1944, Needham gave a description of a larval cast-off skin, which he referred to *Zonophora* by a process of exclusion. In 1966, Belle published photographs of the exuviae of *Z. batesi* and *Z. calippus*, while he gave a brief description of the exuviae of the latter species. The reference of this exuvial material to these two species was based on the difference in size and on the fact that the two species were the only regional ones of the genus occurring in the well-explored surroundings of the airport Zanderij of Surinam. Some half-grown larvae of *Zonophora* were also secured by sifting mud or silt removed from the bottom and sloping banks of the creeks crossing the gallery forests in the surroundings of Zanderij. The gizzard of these larvae was recently examined by me. The result was most surprising as the proventriculus exhibited an unexpected specialized armature, essentially different from that hitherto found in the Gomphidae.

In figs. 1—5 the complete proventriculus of a half-grown larva of *Z. batesi* is shown. Contrary to what is normally found in the Gomphidae, there are two pairs of dissimilar, elevated, sclerotized areas (dental folds) in juxtaposition, one dorsal pair consisting of pyramid-shaped folds and one ventral pair consisting of molar-shaped folds. Each of the folds has a specialized dentition of large, posteriorly directed teeth and, on the posterior end, numerous minute posteriorly directed teeth.

In shape, the dental folds of *Zonophora* much resemble those of *Aphylla* (cf. Beatty, 1956), but

the occurrence of numerous minute teeth on these folds seems to be confined to *Zonophora* (and some Aeshnidae and Lestidae, cf. Bullens, 1966). In the Gomphidae, this aberrant proventricular armature apparently can be employed as a taxonomic character.

**Characterization.** — The genus *Zonophora* is characterized by the following combination of features:

In both sexes:

(1) Numerous intermedian cross-veins in hind wings.

(2) No trigonal supplements and sectors of Rs and M<sub>4</sub>.

(3) Vein A<sub>1</sub> in hind wings well-developed, the proximal angle at the point of separation of A<sub>1</sub> from fused portion A<sub>1</sub> + Cu<sub>2</sub> a right angle or nearly so, the distal angle at same point obtuse.

(4) Discoidal triangles and subtriangles of fore wings more or less similar to those of hind wings; the discoidal triangles elongated in axis of wing and generally once crossed (occasionally two cross-veins); the subtriangles uncrossed.

(5) Pterostigma in hind wings somewhat longer than that in fore wings.

(6) Meso- and meta-paraptera conspicuously produced in an acute point.

(7) Vertex with conical process behind each lateral ocellus.

(8) Occiput angled at rear.

(9) Ventral tergal margins of abdominal segments 8 and 9 not expanded.

In the male:

(10) Anal triangle in hind wings not reaching backward to anal angle of wing.

(11) Superior caudal appendages twice to three times as long as abdominal segment 10 and incurved at tip; inferior caudal appendage about as long as abdominal segment 10 and with two branches widely spread apart.

In the female:

(12) Vulvar lamina reaching from a point one-third the way along ninth sternum to apex of ninth sternum; its posterior margin medially excised.

In the larva:

(13) No dorsal hooks on abdomen.

(14) Abdomen with lateral spines only on abdominal segments 8 and 9.

(15) Caudal appendages about three-and-one-half times as long as abdominal segment 10.

(16) Lateral lobes of labium with incurving teeth along inner margin and with a strong end hook.

(17) Gizzard with two pairs of differentiated dental folds bearing undifferentiated large teeth and numerous minute teeth.

DISPOSITION OF SPECIES AND INFRAGENERIC GROUPS  
(figs. 6—30)

There are excellent characters available for separating the species and subspecies of the genus *Zonophora* into five groups. The members of each group exhibit a striking resemblance in the shape of some structures although some of the statements concerning the shape of these structures will have to be taken with due allowance for individual variation.

(1) The *campanulata* group, comprising *Z. campanulata campanulata* (Burmeister) with its subspecies *Z. campanulata machadoi* St. Quentin and *Z. campanulata annulata* subsp. nov., and *Z. diversa* spec. nov.

The distal segment of the penis has a pair of short and inconspicuous tusk-like spines. The anterior hamules of the male have a well-developed, finger-like, internal lobe. The vulvar lamina is more or less parallel-sided and long, reaching to the apex of the ninth sternum; the tip of the vulvar lamina exhibits much variation, the divisions being sometimes widely spread out (cf. Schmidt, 1941).

The wings have no basal subcostal cross-vein and no extra cubito-anal cross-vein. There is, normally, no traversing cross-vein in the supratriangles (cf. Belle, 1963, Verification tables). The hind wings have sometimes an open anal loop, i.e. open at the proximal side (cf. Schmidt, 1941), but generally an ill-defined anal loop of three to five cells.

There are no distinct morphological differences between *Z. campanulata* and its subspecies. The distinction is based only on colour differences. *Z. c. campanulata* is the darkest of the three. The pale markings on the sides of the pterothorax are grey-green. The abdomen is predominantly dark brown. The tergite of the segments 3 to 8 is densely set with minute black denticles, in particular on the basal part of the segments. The two subspecies *Z. c. machadoi* and *Z. c. annulata* have distinct greenish yellow and yellow markings which are extensive and very striking on the abdomen. The abdominal segments 3 to 8 of the two subspecies are scantily set with minute black denticles.

*Z. diversa* does exhibit great colour and morphological differences with *Z. campanulata* and its subspecies. The superior lobe of the anterior

hamules of the male is vestigial in *diversa*, well-developed in *campanulata*.

(2) The *calippus* group, comprising *Z. calippus calippus* Selys, *Z. calippus spectabilis* Campion and *Z. calippus klugi* Schmidt.

The distal segment of the penis has a pair of short flagella. The anterior hamules of the male are much smaller than those of the *campanulata* group; the internal lobe is small and the superior lobe is long and slender. The vulvar lamina is smaller and more slender than that of the *campanulata* group, and it exhibits but little variation.

The wings have, normally, a basal subcostal cross-vein and generally extra cubito-anal cross-veins. The anal loop in the hind wings is generally open at the proximal side. The supratriangles often have a traversing cross-vein, in the females more frequently so than in the males.

The three members of the group are subspecifically distinct only. They can be discerned on the ground of their coloration. Slight differences are found in the configuration of the anterior hamules of the males but no structural differences are found in the shape of the vulvar laminae.

*Z. c. klugi* is somewhat more robust than the other two. The superior lobe of the anterior hamules is very long and slightly upcurved at the tip. *Z. c. klugi* is also the darkest of the group. The pale frontal band on the superior surface of the frons is medially interrupted by a pitch black band that is broader in the female than in the male.

*Z. c. spectabilis* is the palest of the group. It is distinguished from the other two by the presence of large pale markings on the abdominal segments 8 to 10. The superior lobe of the anterior hamules is widened at the tip.

(3) The *batesi* group, comprising *Z. batesi* Selys and *Z. wucherpfennigi* Schmidt.

The distal segment of the penis has a pair of very long flagella. The anterior hamules of the male are as large as those of the *campanulata* group; the superior lobe is short and stout; the inferior lobe is much larger than that of the *campanulata* group; the internal lobe is very small. The vulvar lamina is widest at base and roughly triangular in outline; it exhibits some variation, the divisions of the tip being often spread out.

The wings have no basal subcostal cross-vein, no extra cubito-anal cross-vein, and no traversing cross-vein in the supratriangles. The anal

loop in the hind wings is open at the proximal side.

The two species of the group differ structurally in the penile organ, the male caudal appendages and vulvar laminae, but the differences are slight and they can be shown more readily by figures than description (cf. Schmidt, 1941). The darkest of the two is *wucherpfennigi*. The seventh abdominal segment of the male is entirely black in this species; it is markedly yellow-coloured at the base in *batesi*. The caudal appendages (stylets) of the female are largely blackish or brownish (paler in middle and black at base) in *wucherpfennigi* (cf. Schmidt, 1941: fig. 12f); they are largely pale-white (black at base) in *batesi*.

(4) The *supratriangularis* group, comprising *Z. supratriangularis* Schmidt and *Z. nobilis* spec. nov. They differ structurally in the male caudal appendages and genital hamules. The distal segment of the penis has a pair of very long flagella. The internal lobe of the anterior hamules of the male is small. The vulvar lamina is about half the length of the ninth sternum.

The wings have no basal subcostal cross-vein but there are extra cubito-anal cross-veins. The supratriangles normally have a traversing cross-vein. The anal loop in the hind wings is open at the proximal side although not always very distinct.

The two species are the palest representatives of the genus.

(5) The *surinamensis* group, comprising *Z. surinamensis* Needham, *Z. solitaria solitaria* Ráencis, *Z. solitaria obscura* Belle, and *Z. regalis* Belle.

The anterior hamules of the male have no internal lobe. The male superior caudal appendages are not knotty at the internal margin. The vulvar lamina is about one-third as long as the ninth sternum.

The wings have no basal subcostal cross-vein and generally no extra cubito-anal cross-vein. The supratriangles occasionally have a traversing cross-vein. The hind wings have a more or less distinct anal loop.

*Z. s. solitaria* is the palest of the group having the lateral sides of the pterothorax largely pale and the dorsum of the eighth abdominal segment with a well-developed pale basal spot. *Z. s. obscura* is the darkest of the group and likewise the darkest representative of the genus. It is distinguished from all congeners by the lack of second pale antehumeral stripes (these stripes are

partly developed in *Z. s. solitaria*). *Z. regalis* is the largest of the genus.

#### SYSTEMATIC SECTION

As considered in this study, the genus *Zonophora* comprises 15 taxa of which three are described as new. The taxa are summarized in table 2, together with their type localities, type status and type locations.

The males of all species and subspecies are known. The females of *diversa*, *nobilis*, *regalis*, *solitaria solitaria*, and *surinamensis* are yet unknown. Their discovery may corroborate the relationships hitherto found between some species.

The recognition of the diverse species and subspecies is comparatively easy. Separate keys have been prepared for the identification of males and females. The key to the males has been based upon the structural characters displayed by the anterior hamules, the penis, the superior caudal appendages, the reticulation of the wings, and some other details. The key to the females has been based on characters displayed by the vulvar lamina and on some coloration details.

#### Key to the (sub)species Males

1. Basal subcostal cross-vein normally present (*calippus* group) ..... 2
- No basal subcostal cross-vein ..... 4
2. Abdominal segments 8 to 10 with extensive yellow markings ..... *calippus spectabilis*
- Abdominal segments 8 to 10 without or with weakly developed yellow markings ..... 3
3. Interrupted median stripe of pale anterior band of frons well-developed and pitch black, its width normally one-third the mid-dorsal length of superior surface of frons or more ..... *calippus klugi*
- Interrupted median stripe of pale anterior band of frons absent, ill-defined or very narrow, its width smaller than one-third the mid-dorsal length of superior surface of frons ..... *calippus calippus*
4. Superior caudal appendages knotty near middle at internal margin; anterior hamules with internal lobe (fig. 9) ..... 8
- Superior caudal appendages not knotty at internal margin; anterior hamules without internal lobe (*surinamensis* group) ..... 5
5. Lateral sides of pterothorax largely pale ..... *solitaria solitaria*

- Lateral sides of pterothorax with well-developed dark stripes ..... 6
- 6. Second pale antehumeral stripes undeveloped ..... *solitaria obscura*
- Second pale antehumeral stripes well-developed ..... 7
- 7. Distal segment of penis with a pair of very short spines ..... *surinamensis*
- Distal segment of penis with a pair of recurved leaf-like plates ..... *regalis*
- 8. Distal segment of penis with short tusk-like spines; internal lobe of anterior hamules well-developed and finger-like (*campanulata* group) ..... 9
- Distal segment of penis with very long flagella; internal lobe of anterior hamules very small ..... 12
- 9. Distal halves of posterior hamules parallel; anterior hamules distinctly trilobate ..... 10
- Distal halves of posterior hamules divergent; anterior hamules not evidently trilobate due to an ill-defined superior lobe .....  
..... *diversa*
- 10. Terminal segments of abdomen without or with weakly developed yellow markings .....  
..... *campanulata campanulata*
- Terminal segments of abdomen with extensive yellow markings ..... 11
- 11. First pale antehumeral stripes connected with pale collar and second pale antehumeral stripes ..... *campanulata machadoi*
- First pale antehumeral stripes neither connected with pale collar nor with second pale antehumeral stripes .....  
..... *campanulata annulata*
- 12. Supratriangles crossed (*supratriangularis* group) ..... 13
- Supratriangles open (*batesi* group) ..... 14
- 13. Superior caudal appendages almost three times as long as mid-dorsum of abdominal segment 10; internal tooth of each appendage at three-fifths the appendage's length ..... *nobilis*
- Superior caudal appendages twice as long as mid-dorsum of abdominal segment 10; internal tooth of each appendage at half the appendage's length ..... *supratriangularis*
- 14. Abdominal segment 7 with large, pale basal marking ..... *batesi*
- Abdominal segment 7 entirely black .....  
..... *wucherpfennigi*

#### Females

- 1. Basal subcostal cross-vein normally present (*calippus* group) ..... 2

- No basal subcostal cross-vein ..... 4
- 2. Abdominal segments 8 to 10 with extensive yellow markings ..... *calippus spectabilis*
- Abdominal segments 8 to 10 without or with weakly developed yellow markings ..... 3
- 3. Pale frontal band on superior surface of frons widely interrupted in middle by pitch black ..... *calippus klugi*
- Pale frontal band on superior surface of frons medially not or not distinctly interrupted by black ..... *calippus calippus*
- 4. Vulvar lamina reaching to apex of ninth sternum ..... 5
- Vulvar lamina half the length of ninth sternum of shorter ..... 9
- 5. Vulvar lamina roughly triangular in outline, widest at base and about twice as long as its basal width (*batesi* group, fig. 17) ..... 6
- Vulvar lamina much longer than wide and subparallel-sided, becoming somewhat narrower towards apex (*campanulata* group, fig. 15) ..... 7
- 6. Caudal appendages (stylets) largely pale-white, black at base; lobes of vulvar lamina distinctly remote at bottom of excision .....  
..... *batesi*
- Caudal appendages (stylets) largely brown, paler in middle, black at base; lobes of vulvar lamina close together at bottom of excision ..... *wucherpfennigi*
- 7. Abdominal segments without or with weakly developed yellow markings .....  
..... *campanulata campanulata*
- Abdominal segments with extensive yellow markings ..... 8
- 8. First pale antehumeral stripe connected with pale collar and second pale antehumeral stripe ..... *campanulata machadoi*
- First pale antehumeral stripe neither connected with pale collar nor with second pale antehumeral stripe ..... *campanulata annulata*
- 9. Second pale antehumeral stripe well-developed; vulvar lamina half the length of ninth sternum (*supratriangularis* group) .....  
..... *supratriangularis*
- Second pale antehumeral stripe undeveloped; vulvar lamina one-third the length of ninth sternum (*surinamensis* group) .....  
..... *solitaria obscura*

#### Treatment of the species

The species have been treated in a sequence, which allows expression of apparent relationships. Under each species a list of syno-

nyms, data on the material studied, description or descriptive notes, and remarks are given.

### *Zonophora campanulata campanulata*

(Burmeister, 1839)

(figs. 6, 9, 15, 19—20, 23, 31—34, 72)

*Diastatomma campanulata* Burmeister, 1839: 833  
(♂). Calvert, 1898: 35, 52, 94, 94—95.

*Zonophora campanulata* Selys, 1854: 80—81 (61—62  
sep.) (♀); 1869: 199—200 (36—37 sep.). Selys &  
Hagen, 1858: 492, 494—496 (232, 234—236, 238  
sep.); pl. 23, fig. 5. Hagen, 1861: 313; 1875: 54.  
Kirby, 1890: 75. Navás, 1916: 73. Campion, 1920:  
137—138, 140. St. Quentin, 1939: 227. Schmidt,  
1941: 77—78, 80, 83, 86, 89—90, 92; figs. 5c, 6c,  
8c, 9d, 10d, 11e, 12c. Needham, 1944: 218—219.  
Belle, 1963: 60—63. Dias dos Santos, 1970: 204.  
St. Quentin, 1973: 338—339; fig. 3.

Material. — Brazil: 1 ♂ (neotype), 1 ♀ (neotype series of *Diastatomma campanulata* Burmeister); Tijuca, 2 ♂, IRSN; Porto Catherina de Santa Leopoldina, 3 ♂, UMMZ; Minas Gerais, Caraça, Sta. Barbara, February 1970, 1 ♂, A.M.M. Machado leg., CM; Espírito Santo, 3 ♂ (1 ♂ ex coll. Fruhstorfer), 1 ♀, MP. — ? Guyana ? : 1 ♂, MP. — ? Surinam ? : 2 ♂, 1 ♀, MP.

This species was described by Burmeister (1839) after a single male from "Brazil". This male must be considered to be identical with the darkest representative of the *campanulata* group since the statement "fusca, subtus dilutior; abdominis segmento septimo fascia basali pallida" in the original description evaluates the specimen. If all its abdominal segments has had extensive pale markings, they should undoubtedly be mentioned in the description.

The location of the type of *D. campanulata* is unknown. Calvert (1898) as well as Belle (1963) were unable to find it. Also further search made by myself was in vain. I am strongly inclined to believe that the original specimen is lost, possibly destroyed by a dermestid infestation (*Anthrenus*). The species, however, has been very well described and figured in the *Monographie des Gomphines* (Selys & Hagen, 1858). In order to stabilize its identity a neotype is here designated.

Neotype designation of *Diastatomma campanulata* Burmeister. — The chosen neotype is a male from a remarkable uniform series placed under *Zonophora campanulata* (Burmeister) in the Selysian collection in Brussels. This series consists of the following specimens:

(1) A male with the pin label "Cl. 2."

(2) A female with the pin labels "Cl. 3" and "*Zonophora campanulata* B ♀", this latter in Selys' handwriting.

(3) A male with the pin labels "122", "122", "Tijuca P.B.", and "*Zonophora campanulata* B. ♂", this latter in Selys' handwriting.

(4) A male with the pin label "Tijuca P.B."

The abbreviation "P.B." may refer to Paul de Borchgrave who has collected Odonata in Tijuca near Rio de Janeiro round-about 1860 (cf. Calvert, 1956: 88, 175—176).

The abbreviation "Cl." may refer to Dr. Clausen from whom Selys received the specimens mentioned in the *Monographie des Gomphines*, p. 496 (236 sep.).

I think, that the male which served for Hagen's figures in this monograph belonged to the above mentioned series. This male should have borne at the pin the (missing) label "Cl. 1" and probably also Selys's identification label of the Tijuca male. The specimens of Dr. Clausen are homotypes as may appear from Selys's (1858) remark in parentheses: "C'est le type de M. Burmeister qui offre les noms les plus grands". The homotype male labelled "Cl. 2" is here designated as neotype of *Diastatomma campanulata* Burmeister, 1839.

*Z.c. campanulata* exhibits some striking variations. The hind wings of none of the present specimens have a distinct open anal loop, due to a rather well-developed vein A2. The hind wings of some specimens have more or less a distinct anal loop of 3 to 5 cells, with the vein A1 angled at the lower distal corner of the anal loop.

The form of the vulvar lamina is also variable, in particular at the tip. The vulvar lamina of the present females approaches that depicted by St. Quentin (1973) but it differs considerably from that depicted by Schmidt (1941).

The female of the neotype series has a vulvar lamina with a damaged tip. As this female was the only one available for Hagen, it apparently served for his figure in the *Monographie des Gomphines* (pl. 13, fig. 1t).

Some data in Selys's redescription of 1854 are incorrect. The measurement for the female abdomen is 50 mm (incl. caud. app.) and not 58 mm (cf. Campion, 1920, foot-note on p. 137). Further, the number of given antenodal cross-veins in the fore wings of the male is 18 instead of 13 (cf. Selys, 1869). The nodal index of the neotype is 14 : 20—20 : 13/13 : 14—15 : 14.

Fraser (1940) published a figure of the penis

of a *Zonophora* male, which he referred to *Z. campanulata*. But judging from the conformation of the penile organ his male belonged to the *batesi* group.

**Remark.** — Caution should be made regarding the locality labels of the specimens in the Martin collection (lodged in the Muséum National d'Histoire Naturelle, Paris) since several of these old labels prove to be unreliable. Some specimens of *Z. c. campanulata* have the pin labels "Surinam" and "Guyana" but these localities may be incorrect since nor Dr. D. C. Geijskes nor I myself have encountered this species during our extensive explorations in Surinam and Guyana. On that account these records have not been inserted in the distribution map.

To further illustrate the unreliability of some locality labels of the Martin collection, in the boxes in which the specimens of *Zonophora* were stored, I found four males of *Phyllogomphoides pacificus* (Selys, 1873) labelled "Minas Gerais" and "Bresil", and a male of *Aphylla cariba* Selys, 1854, labelled "Bresil".

#### ***Zonophora campanulata machadoi***

St. Quentin, 1973

(figs. 21, 24, 35—36)

*Zonophora machadoi* St. Quentin, 1973: 338—340;  
figs. 4a—b (♂). Kiauta, 1981: 35, 60.

**Material.** — Brazil: Minas Gerais, Belo Horizonte, 18 March 1979, 1 ♂, AC; Tabueos, Ibirité (near Belo Horizonte), 22 March 1979, 1 ♂, CJ, both G. Jurzitz leg.; Ibirité, 21 March 1979, 1 ♀, A. B. M. Machado leg., CM.

This subspecies was described by St. Quentin (1973) after a single male from Belo Horizonte, Brazil. The female is described below.

Female (hitherto unknown; degutted and treated with acetone). — Total length, 64 mm; abdomen, 49 mm (including caudal appendages, 4.3 mm); hind wing, 45 mm; costal edge of pterostigma in fore wing, 6.0 mm, in hind wing, 6.5 mm.

Coloration resembling that of male holotype. Face brown with conspicuous bright yellow band covering suture between postclypeus and vertical part of frons. Labium with pale cross-band in midfield. Anteclypeus becoming paler on outer edges. Superior surface of frons brown with oblong yellow spot on either lateral side.

Colour pattern of prothorax and pterothorax very similar to that of male. Abdomen relatively

shorter than that of male. Pale markings on sides of abdominal segments 8 and 9 much smaller than in male, and abdominal segment 10 entirely dark brown (fig. 36).

Proportional length of abdominal segments 7, 8, 9, and 10 approximately as 45 : 30 : 20 : 10, with the caudal appendages 34 on same scale. Vulva lamina shaped as shown in fig. 21.

Pterostigma surmounting eight cells. No basal subcostal cross-vein. No extra cubito-anal cross-vein. No traversing cross-vein in supratriangles. No anal loop in hind wings. Nodal index 14 : 20—22 : 13/13 : 13—13 : 15. Second primary antenodal cross-vein the eighth in fore wings, the sixth in hind wings. Intermedian cross-veins 7—9/3—3 in fore and hind wings, respectively. Hind wings with six (left) and seven (right) paranal cells, six (left) and seven (right) postanal cells, and area posterior to Cu<sub>2</sub> six to seven cells wide.

#### ***Zonophora campanulata annulata***

subspec. nov.

(figs. 22, 23, 37—38)

**Material.** — Brazil: Gioás, Jataí (Jatahy), 3 ♂ holotype and paratypes), 1 ♀ (allotype), MP.

This subspecies, though very similar in its morphology to *Z. c. campanulata* and *Z. c. machadoi*, is readily distinguished from both by the aberrant colour pattern of the pterothorax, which, in lateral view, shows a conspicuous pair of well-developed pale twin-stripes, the first pair being formed by the second pale antehumeral stripe and the first pale lateral stripe, and the second pair by the second and third pale lateral stripes. The colour pattern of the dorsum of the pterothorax is most like that of *Z. c. campanulata* by the isolated pale antehumeral stripes and pale collar, while the abdomen greatly resembles that of *Z. c. machadoi* by the annulated appearance owing to the extensive pale markings at the base of the segments.

According to some of the hitherto used characters, the colour differences mentioned above are important enough to consider the present examples from Jataí a distinct variety or subspecies. I prefer to regard them as a subspecies since they are forming a homogeneous series, and since they seem to be the only form occurring in that part of the distribution area. However, as long as our knowledge is restricted to the scarcely available material it is difficult to indicate the value of the characters used for the subspecific distinction. The features often vary

in some widely ranging gomphid species to such a degree that it remains to be seen whether the status of the subspecies introduced will stand the test of future collecting.

Male (holotype; abdomen broken on segment 6 and between segments 3 and 4; left superior caudal appendage broken off and lost). — Total length, 66 mm; abdomen, 50 mm (incl. caud. app., 4 mm); hind wing, 42 mm; costal edge of pterostigma in fore wing, 5.6 mm, in hind wing, 6.0 mm.

Face yellowish green but brown along border of labrum and just below frontal ridge of frons. Superior surface of frons yellowish green on anterior half, brown on basal half. Vertex black. Occipital plate and rear of occiput yellow-brown. Rear of head yellowish brown. Base of mandibles, genae, labium and adjacent mouth parts pale brown.

Prothorax dark brown with greenish yellow markings. Median lobe with pale middorsal twin-spot and pale spot on each lateral side; posterior lobe with pair of pale oblong spots.

Pterothorax dark brown to black, the pale markings greenish yellow, becoming yellow on metepimeron. Colour pattern of pterothorax shaped as shown in accompanying diagram. Middorsal carina and antealar sinus pale. Pale collar and first pale antehumeral stripe narrow. Second pale antehumeral stripe and pale lateral stripes rather broad.

Femora reddish-brown but inner side of first pair green. Tibiae, tarsi, and claws dark brown. Lamina tibialis of first tibiae one-seventh the tibial length.

Wings clear, its venation pale brown, becoming darker on posterior margin of wings. Pterostigma brown-yellow, surmounting 6— $6\frac{1}{2}$  cells. Brace vein present. No basal subcostal cross-vein. A single cubito-anal cross-vein in addition to inner side of subtriangle in all wings. Supratriangle in right hind wing with a traversing cross-vein, in other wings uncrossed. Subtriangles open. Discoidal triangles two-celled. Nodal index 12 : 18—16 : 11/13 : 12—11 : 12. Second primary antenodal cross-vein the seventh in left fore wing, the sixth in other wings. Intermedian cross-veins 8—8/4—4 in fore and hind wings, respectively. Hind wings with open anal loop (open at proximal side), a four-celled anal triangle, five (right) and six (left) paranal cells, five (right) and six (left) postanal cells, and area posterior to Cu<sub>2</sub> five cells wide.

Abdomen dark brown to black, the pale

markings yellow. Segment 1 pale on lower part of lateral sides and along dorsal posterior margin. Segment 2 pale on lower parts of lateral sides, on auricles, and just above auricles. Segments 3 to 8 with large pale basal markings which become successively larger on 3 to 8, laterally reaching to supplementary transverse carina on 3, and extending to beyond this carina on 4 to 8. Segment 9 with pale lateral markings extending along lower part of side to apex of segment. Segment 10 largely pale. Tuberles with externo-lateral pale spots. Inferior appendage black. Superior appendages pale yellow but extreme base brown.

Female (allotype). — Total length, 69.5 mm; abdomen, 53 mm (incl. caud. app., 4 mm); hind wing, 46 mm; costal edge of pterostigma in fore wing, 6.4 mm, in hind wing, 6.6 mm.

Very similar to male holotype in stature and coloration but abdomen stouter. Proportional length of abdominal segments 7, 8, 9, and 10 approximately as 40 : 23 : 19 : 10, with the caudal appendages (stylets) 28 on the same scale.

Pterostigma surmounting 5½—6½ cells. No basal subcostal cross-vein. No extra cubito-anal cross-vein. No traversing cross-vein in supratriangles. Second primary antenodal cross-vein the eighth in left hind wing and right fore wing, the seventh in other wings. Hind wings with a weak development of an anal loop of four cells.

The male paratypes are very similar to the holotype. All their wings have uncrossed subtriangles and supratriangles. The triangles have one dividing cross-vein. The anal triangles are four-celled. The hind wings of one of the male paratypes have a weak development of an anal loop of four cells.

#### *Zonophora diversa* spec. nov. (figs. 39—50)

Material. — Argentina: Misiones, Dos de Mayo, January 1982, 2 ♂ (paratypes), J. Foerster leg., AC and CJ. — Brazil: Santa Catarina, Nova Teutonia, 2 March 1942, 1 ♂ (paratype, AC), 3 March 1942, 2 ♂ (paratypes), 4 March 1942, 1 ♂ (paratype), UMMZ; same locality, January 1946, 1 ♂ (holotype, CC), all Fritz Plaumann leg. — Paraguay: Alto Parana, Taquerí (Tacurí), near Río Nacunday, 20 February 1980, 1 ♂ (paratype), H. Miers leg., CM.

This species is closely related to the type-species of the genus, *Z. c. campanulata*, but it is rather easily distinguished in the male sex by the stouter superior caudal appendages, the ill-de-

fined superior lobe of the anterior hamules, and the divergent distal halves of the posterior hamules.

The female is unknown.

Male (holotype). — Total length, 70 mm; abdomen, 54 mm (including caud. app., 4 mm); hind wing, 47 mm; costal edge of pterostigma in fore wing, 5.0 mm, in hind wing, 5.4 mm.

Face greenish-yellow but labrum black along free-border. Superior surface of frons black at base, greenish yellow on its three-fifths anterior portion, yellow on anterior ridge. Vertex black. Occipital plate yellowish-green, its posterior margin slightly and evenly convex, and heavily fringed with brown hairs.

Prothorax dark brown, the middle lobe with reddish brown lateral markings and a more yellowish mid-dorsal twin-spot, the hind collar dark reddish brown.

Pterothorax blackish brown with greenish yellow markings, its colour pattern shaped as shown in fig. 46. Femora blackish brown, save for a streak of yellowish brown on outer basal two-thirds portion of third femora. Tibiae and tarsi black. Claws dark reddish brown.

Wings hyaline, its venation brown including frontal margin of costa. Pterostigma brown, surmounting 5½—6½ cells. Brace vein present. No basal subcostal cross-vein. Nodal index 14 : 18—18 : 14/13: 14—13 : 15. Second primary antenodal cross-vein the seventh in right hind wing, the eighth in other wings. Intermedian cross-veins 7—6/4—5 in fore and hind wings, respectively. No extra cubito-anal cross-vein. All subtriangles and supratriangles free from cross-veins. All discoidal triangles two-celled. Hind wings with an ill-defined anal loop of four (left) and five (right) cells, an anal triangle of six cells (two cells small), six paranal cells, seven (left) and six (right) postanal cells, and area posterior to Cu<sub>2</sub> six cells wide.

Abdomen black with yellow markings, its colour pattern shaped as shown in fig. 43. Segment 10 with brownish yellow mid-dorsal spot. Sterna of segments 6 to 8 brown to blackish brown but yellow on basal one-fifth; sternum of 8 with an extra, oblong yellow spot on either side half-way the sternum. Inferior caudal appendage black. Superior caudal appendages dark brown. Caudal appendages and accessory genitalia shaped as shown by the accompanying figures.

The following colour differences between the

holotype and the paratypes from Nova Teutonia are noteworthy. One male has the black band along the free border of the labrum not developed in the middle and at either side; two males have the black basal band on the superior surface of the frons medially interrupted by greenish yellow; in three males the black markings on the dorsum of the pterothorax are reduced; one male has the black antehumeral stripes almost lacking; one male has the pale markings of the prothorax yellow.

The coloration of one of males from Argentina is very similar to that of the holotype. The other Argentine male has the black humeral and femoral stripes largely undeveloped.

The male from Paraguay exhibits the most striking colour differences. Its labrum is entirely green. The black basal band on the superior surface of the frons is reduced to two narrow streaks at the level of the antennae. The vertex has a greenish yellow median stripe between the lateral ocelli. The occipital plate is yellow. The hind collar of the prothorax is entirely reddish brown. The pterothorax is almost entirely green; the dorsum is entirely green; the black humeral, interpleural and metapleural stripes are developed only near the subalar carinae. The terminal segments of the abdomen have extensive yellow markings; segments 5 and 6 are yellow on the apical half; the yellow marking of 7 reaches to a point three-quarters the way along the segment on the sides; segment 8 is yellow on slightly more than the basal half; segment 9 is yellow on the basal half; segment 10 is yellow with black baso-lateral markings and a black hind margin, the tubercles are yellow.

### *Zonophora calippus calippus* Selys, 1869

(figs. 7, 10, 16, 73)

*Zonophora calippus* Selys, 1869: 199—200 (36—37 sep.) (♂, ♀). Hagen, 1875: 54. Kirby, 1890: 75. Campion, 1920: 140. Schmidt, 1941: 76—77, 80—81, 84. Needham, 1944: 171, 218—219, pl. 16, figs. 18a—f. Belle, 1963: 60, 62—63, 65—69; 1966: 64, figs. 97—98, pl. 11b (exuviae); 1972: 217, 237—238, fig. 39. St. Quentin, 1973: 338—339. Kauta, 1979: 267—269.  
*Zonophora calippus calippus* Schmidt, 1941: 84—85, figs. 5d, 6a, 8a, 8f, 9a, 11a.

Material. — Brazil: Pará, Santarém, Amazon River (Mahica), December 1920, 1 ♂, A. H. Fassl, leg.; UMMZ; Pará, Fordlandia, February 1957, 1 ♀; Pará, Belem (Utinga Forest), February 1957, 2 ♂, all A.B.M. Machado leg.; Paraíba, João Pessoa (Buracinho Forest), May 1976, 1 ♂, Kesselring leg., CM.

— Guyana: Georgetown, March 1955, 1 ♂, M. Alvarenga leg., CM.

This species was described by Selys (1869) after a single pair from Santarém, Brazil. Needham (1944) recorded it from Surinam, Belle (1972) from Venezuela, and St. Quentin (1973) from Guyana. Some specimens of *Zonophora* already placed on record by St. Quentin (1973) were kindly sent to me for restudy by Prof. Machado.

The present male from Santarém has the pale frontal band on the superior surface of the frons narrowly interrupted in the middle by black; the pale band is normally not or not distinctly interrupted in the middle. The male from Paraíba has the mid-lateral pale stripe on either side of the pterothorax almost absent.

St. Quentin (1973) referred the female from Fordlandia (100 km south-west of Santarém) to the genus only, possibly due to the fact that in this specimen the wings have no basal subcostal cross-vein.

The first and second pale antehumeral stripes are often confluent in *Z. c. calippus*. The occipital ridge of the female has generally a pair of denticles which are often unsymmetrically situated or partly developed.

The larva of *Z. c. calippus* was described from Surinam by Belle (1966).

### *Zonophora calippus spectabilis* Campion, 1920 (fig. 12)

*Zonophora spectabilis* Campion, 1920: 138—140; pl. 7, fig. 15 (♂). Schmidt, 1941: 76—77, 80—81, 86. Belle, 1963: 61—62, 66—68; 1972: 237—238; figs. 36—38 (♀). Kimmens, 1969: 298. St. Quentin, 1973: 338—339. Paulson, 1977: 176.

*Zonophora calippus spectabilis* Schmidt, 1941: 86—88, 92; figs. 7c, 11c. Needham, 1944: 218.

Material. — Bolivia: Santa Cruz, (San José de) Chiquitos, Roboré (300 m), 26 December 1953, 1 ♂, W. Forster leg., IZM. — Brazil: São Paulo, Itapetininga, 10 February 1978, 1 ♂ (very teneral), E. Dente leg., CM.

*Z. c. spectabilis* was described by Campion (1920) after a single male from Sapucay, Paraguay. Belle (1972) recorded this subspecies from Bolivia. Paulson (1977) included Argentina in its range. I accordingly wrote to Dr. Paulson on May 24, 1980, about this record in his list and he kindly replied, under date of June 8, 1980, that he had wrongly entered on his cards Needham's (1944) record that Campion described

*spectabilis* from "Argentina" (instead of Paraguay). The presence of *Z. c. spectabilis* in Brazil was not known before.

The yellow marking of the tenth abdominal segment of the male from Brazil is much more extended than as shown by Schmidt (1941) for a male from Paraguay. The male from Bolivia, on the contrary, has the yellow markings on the abdominal segments 8 to 10 smaller, and it lacks the lance-shaped yellow extension on the mid-dorsum of the segments 8 and 9.

### *Zonophora calippus klugi* Schmidt, 1941 (fig. 11)

*Zonophora calippus klugi* Schmidt, 1941: 80—81, 85—86; figs. 4a, 5a—b, 7a, 8g, 9b, 10a, 11b, 12a (♂, ♀); 1958: 235, 251. Rácenis, 1959: 492. St. Quentin, 1973: 339.

*Zonophora klugi* Belle, 1963: 60—63, 66—68; pls. 3—4; 1972: 238. St. Quentin, 1973: 338—339.

Material. — Brazil: Amazonas, Tefé, January 1958, 1 ♂, Carvalho leg.; Acre, Feijó, no date, 1 ♂; Território de Rondônia, Pôrto Velho, 16 November 1962, 1 ♀, both Bokermann leg., CM; Território de Rondônia, Madeira-Mamoré River, near Jaci Paraná (km 87—91), 7 February 1922, 1 ♂, J. W. Strohm & J. H. Williamson leg.; Amazonas, São Paulo de Olivença (Alto Rio Solimões), April 1932, 1 ♂, F. Wucherpfennig leg., UMMZ. — Ecuador: Napo-Pastaza (Río Napo watershed), Río Ilapulin, Jatún Yacu (800 m), 13 March 1937, 1 ♀; same locality (700 m), 28 March 1937, 2 ♀, all Wm Clark-Macintyre leg., UMMZ.

*Z. c. klugi* was described by Schmidt (1941) after several males and females from Mishiyacu, Peru. St. Quentin (1973) recorded it from Brazil. The subspecies is new to the fauna of Ecuador. Belle (1963) selected the male with the Senckenberg's catalogue number 24000 as the lectotype.

The triangular envelope with the male taken by Strohm & Williamson is labelled "State of Matto Grosso" instead of Território de Rondônia. The envelope has the field note: "Flew into wind-shield of motor-car (a fine wire screen which caught and held many kinds of insects)". The inserted male has the pitch-black stripe which divides the pale frontal band on the superior surface of the frons about one-tenth the width of the frons. This stripe is generally one-fourth the width of the frons in the males of this subspecies. The male has further three small yellow spots on either side of abdominal segment 8. This segment is entirely black in the other examples of this subspecies.

The present females from Ecuador are the

largest specimens of the series; their measurements are; abdomen, 49 mm (incl. caud. app.); hind wing, 45—46 mm.

The male from Tefé was referred to *Z. batesi* by St. Quentin (1973).

**Zonophora batesi** Selys, 1869  
(figs. 1—5, 8, 13, 17, 74)

*Zonophora batesi* Selys, 1869: 198—200 (35—37 sept.) (♂). Hagen, 1875: 54. Kirby, 1890: 75. Campion, 1920: 137. Schmidt, 1941: 76, 80, 82, 84, 92—94, 96; figs. 4c, 6d, 8d, 9e, 11f, 12d, 12g. Needham, 1944: 218—219; pl. 16, fig. 19a. Calvert, 1948: 61—62. Belle, 1963: 60—65, 67; 1966: 62—64; fig. 95—96; pl. 11b (exuviae); 1972: 217, 236; 1977b: 292. Geijskes, 1971: 666. St. Quentin, 1973: 338—339.

*Zonophora batesi* St. Quentin, 1973: 338.

*Zonophora bodkini* Campion, 1920: 136—138; pl. 7, figs. 10—14 (♀). Schmidt, 1941: 76, 78, 92—94, 96. Needham, 1944: 218. Calvert, 1948: 62. Belle, 1963: 61, 65. Kimmins, 1969: 291. Geijskes, 1971: 666.

Material. — Brazil: Amapá, Serra do Navio, October 1957, 1 ♀, Lenko leg.; Pará, Ananindeua, 7 September 1964, 1 ♂, Souza leg., CM. — Guyana: Tumatumari, 5 February 1912, 1 ♂, 1 ♀, L. A. & E. B. Williamson, and B. J. Rainey leg., UMMZ. — Surinam: Coropina Creek (upper part), Dauwdropkamp, 6 November 1955, 1 ♀, J. Belle leg., ML.

*Z. batesi* was described by Selys (1869) after a single male from Fonte Boa, Brazil. Campion (1920) recorded it (under *Z. bodkini*) from Guyana, Needham (1944) from Surinam and Geijskes (1971) from French Guyana. The larva of this species was described by Needham (1944) and Belle (1966).

Some features of the female here recorded from Surinam were already published by Belle (1963) but its locality data were not yet put on record.

**Zonophora wucherpfennigi** Schmidt, 1941

*Zonophora wucherpfennigi* Schmidt, 1941: 80, 84, 94—96; figs. 3a, 4d, 5e, 8e, 11g, 12e—f (♂, ♀). Belle, 1963: 62—63, 69. St. Quentin, 1973: 338. *Zonophora batesi wucherpfennigi* St. Quentin, 1973: 338—339.

Material. — Brazil: Pará, Itaituba, November 1961, 1 ♀, J. B. Ferreira leg. (No. 90 of St. Quentin, 1973), CM.

Lectotype designation of *Zonophora wucherpfennigi* Schmidt. — The type series of this Brazilian species belonged to the collection

of Schmidt and consisted of two males from Manicoré and one female from Tefé. Schmidt did not designate a holotype so that a lectotype must be selected now. The penile organ of one of two males has been extruded and figured by Schmidt (his fig. 11g). The male which served for this figure is here designated as the lectotype of *Zonophora wucherpfennigi* Schmidt, 1941. This lectotype is in the collection of Dr. S. Asahina, Tokyo, because Schmidt's collection has been incorporated into it.

The female of *Zonophora wucherpfennigi* in the collection formerly owned by Schmidt was tentatively referred to this species. The female from Itaituba, referred to *Z. wucherpfennigi* by St. Quentin (1973), was kindly lent to me for re-study by Prof. Machado. It fits fairly well the description and figures of the female from Tefé given by Schmidt (1941) except for the large pale basal marking of the seventh abdominal segment, which in the female from Itaituba is reduced to a pair of dorso-lateral spots. In the female of *batesi* this pale basal marking is mid-dorsally interrupted by a black line. In my opinion the females from Tefé and Itaituba are both conspecific with *wucherpfennigi*.

**Zonophora surinamensis** Needham, 1944  
(figs. 26—30, 76)

*Zonophora surinamensis* Needham, 1944: 219—221; pl. 16, figs. 17a—b (♂). Belle, 1963: 60, 62, 69; 1966: 62—63; figs. 93—94; pl. 11a; 1972: 238; 1976: 206. Rácenis, 1970: 28. St. Quentin, 1973: 338.

*Z. surinamensis* was described by Needham (1944) after a single male collected in Brazil at the Rio Mapaoni, a left-tributary of the Jari River, in the Serra de Tumucumaque. Belle (1972) recorded it from Surinam.

The original description of this species was elucidated by depictions of the conventional dorsal and lateral views of the male caudal appendages only. Belle (1966) published figures of the accessory genitalia of the male holotype in lateral and ventral views. The increasing number of related species, however, makes it advisable to pay more attention to some critical structures, hence the here offered original camera lucida drawings of the penis, penis guard, and anterior genital hamule of this species. A diagram of the thoracic colour pattern is also added. The male of *Z. surinamensis* taken in Surinam (cf. Belle, 1972) has served to furnish the

present illustrations. As clearly appears from the figures, the colour design of the pterothorax resembles greatly that of *Z. regalis* while the penis agrees with that of *Z. campanulata* in that the tip possesses a pair of very short spines.

Contrary to the holotype, the male from Surinam has no extra cubito-anal cross-vein in the wings, whereas the anal loop in either hind wing consists of four cells only (five cells in the type).

***Zonophora solitaria solitaria* Rácenis, 1970**  
(figs. 51—54)

*Zonophora solitaria* Rácenis, 1970: 26—28; figs. 2—3 (♂). De Marmels, 1980: 128; 1983: 8.

This species was described by Rácenis (1970) after a single male from Guayaraca-Auyantepui, Venezuela.

Mr. De Marmels, who investigated the male holotype of *Z. solitaria* Rácenis in the Instituto de Zoología Agrícola in Maracay, generously provided me with valuable sketches of the markings of some important details (figs. 51—54). He also compared the type with that of *Z. obscura* Belle and wrote from Egg in Zwitserland, July 29, 1981: "It seems rather different from your *obscura*, at least at a first sight. The *solitaria*'s thorax sides are nearly uniformly green olivaceous, almost lacking black bands. On dorsum of (abdominal) segment 8 there is a big tripartite yellow basal spot. Pterostigma is darker brown. The anal appendages seem identical, as well as the (accessory) genitalia although I did not extract the penis. Rácenis's (or his assistant's) figures are always very accurate".

***Zonophora solitaria obscura* Belle, 1976**  
(figs. 18, 55)

*Zonophora obscura* Belle, 1976: 197, 203—206; figs. 16—24 (♂). Kiauta, 1981: 35, 49. De Marmels, 1983: 8.

Material. — Venezuela: Bolívar, at km 125 from El Dorado to Santa Elena (1100 m), 25 September 1967, 1 ♀, Rosales, Gelvez & Rodríguez leg., IZM.

This subspecies was described by Belle (1976) after a single male from Sta. Elena, Venezuela. Mr. De Marmels, who compared the male holotype of *Z. obscura* Belle with that of *Z. solitaria* Rácenis, did find structural differences neither in the caudal appendages nor in the accessory genitalia, although he did not extract the penis of *solitaria*. The colour differences between the two males, however, are great and they seem

important enough to consider *obscura* a subspecies of *solitaria*, at least provisionally. The distinction may be apparent from the following comparison:

(1) In *obscura*, the second pale antehumeral stripes are not developed; in *solitaria*, they are developed on the lower (anterior) part of the thoracic dorsum.

(2) In *obscura*, the dark lateral stripes of the pterothorax are well-developed, the first and second dark lateral stripes being entirely or largely confluent; in *solitaria*, the lateral sides of the pterothorax are almost uniformly pale, lacking distinct black bands.

(3) In *obscura*, the abdominal segment 8 is entirely black; in *solitaria*, it has a large tripartite yellow basal spot.

Differences are also found in the coloration of the face, the vertex and the occipital plate. If a comparison is made with the sketches of Mr. De Marmels (figs. 52, 54) the following differences are noteworthy:

(4) In *obscura*, the vertical part of the frons and the postclypeus are black except for a pale cross-stripe covering the fronto-clypeal suture; in *solitaria*, they are largely pale.

(5) In *obscura*, the vertex and occipital plate are entirely black; in *solitaria*, each of them has a pale central spot.

Although *obscura* is a darker species than *solitaria*, the pterostigmata of *obscura* are lighter brown than those of *solitaria*.

The female of *Z. s. obscura* is described below.

Female (hitherto unknown; abdomen partly flattened; tips of fore wings broken off but not lost). — Total length, 63 mm; abdomen, 47 mm (incl. caud. app.); hind wing, 46 mm; costal edge of pterostigma in fore wings, 5.8 mm, in hind wings, 6.0 mm.

Similar to male but labrum with an extra pale mid-basal spot, vertex with a pale spot between conical processes (tips of these processes yellow), and pale metepisternal stripes weakly developed near subalar ridge. Pale baso-lateral spots of abdominal segments 3 to 6 reduced, reaching to supplementary transverse carina on 3, being nearly absent on 6. Pale basal marking on dorsum of 7 well-developed. Occipital plate with several whimsical grooves in middle part, the crest densely set with long, stiff, black hairs (broken off in middle part of crest). Caudal appendages (stylets) black-brown at bases, becoming paler (brown) towards tips. Abdominal segments 7, 8, 9, and 10 approximately in ratio

37 : 24 : 17 : 10, with the caudal appendages (stylets) 19 on the same scale. Vulvar lamina one-third the length of ninth sternum, in ventral view triangular in outline, projecting in an oblique direction downwards and rearwards (possibly due to the fact that the abdomen is partly flattened), its posterior margin medially excised U-shaped for about two-thirds the length of vulvar lamina, the lobes triangular and acute.

No basal subcostal cross-vein. Nodal index 16 : 21—21 : 16/16 : 17—17 : 16. Second primary antenodal cross-vein the eighth in right hind wing, the seventh in other wings. Cell between first and second postnodal cross-veins divided by a cross-vein subparallel to costa. Intermedian cross-veins 10—9/4—5 in fore and hind wings, respectively. Supratriangle in left fore wing with one cross-vein, in other wings open. No extra cubito-anal cross-veins. Subtriangles open. Discoidal triangles two-celled. Hind wings without anal loop, with six paranal cells, six postanal cells, and area posterior to Cu<sub>2</sub> five to six cells wide.

#### *Zonophora regalis* Belle, 1976

*Zonophora regalis* Belle, 1976: 197, 200—203; figs. 5—15 (♂). Kauta, 1981: 35, 49.

This large species was described by Belle (1976) after three males from La Ceiba del Venturi, Venezuela.

The anal loop in the hind wings of the holotype is two-celled owing to the fact that one of the dividing cross-veins is only partly developed. The anal loop in the hind wings of the two paratypes consists of three cells.

Mr. De Marmels kindly informed me, under date of February 8, 1982, that all the Odonata from the Rácenis collection formerly in Caracas have been transferred to the Instituto de Zoológia Agrícola in Maracay. The holotype of *Zonophora regalis* Belle, consequently, is now in that institution.

#### *Zonophora supratriangularis* Schmidt, 1941 (figs. 14, 56, 75)

*Zonophora supratriangularis* Schmidt, 1941: 77—78, 80—81, 83, 88: figs. 1, 2a, 4b, 6b, 7b, 8b, 9c, 10b—c, 11d, 12b (♂, ♀). Belle, 1963: 61—63, 65 (*supratriangularis* is a misprint for *supratriangularis*), 69. Rácenis, 1966: 8. St. Quentin, 1973: 338.

Material. — Brazil: Amazonas, Manaus (Manáos), 17 July 1976, 1 ♀, collector unknown; same locality, 9 August 1977, 1 ♂, A. Castrilón leg., CM. — Venezu-

ela: Territorio Federal Amazonas, San Fernando de Atabapo, 24 February 1957, 1 ♂, J. Rácenis leg., IZM.

Schmidt (1941) described this species after five males and three females from several localities in Brazil. He again (see *Z. wucherpfennigi*, ante) did not designate a holotype. After Schmidt, in case of type designation in the future, preference should be given to the male from Borba since the pair from this locality has served him to furnish most of the figures of this species. Of the male from Borba illustrations of the wings, caudal appendages and accessory genitalia are given, but of the male from Tefé depictions of the whole insect (in side view) and of the basal abdominal segments (in dorsal view) are offered. In my opinion, there is no principle objection to select the male from Tefé as lectotype.

Lectotype designation of *Zonophora supratriangularis* Schmidt. — There are five "cotypes", three males and two females, of this species among the material of the Ris collection in the Natur-Museum Senckenberg, Frankfurt-am-Main. Each of the specimens is stored in a triangular envelope with the printed label "det. Dr. Erich Schmidt". The five envelopes possess the Senckenberg's catalogue numbers 24025 till 24029. Of these syntypes, the male numbered 24026 is here designated as the lectotype of *Zonophora supratriangularis* Schmidt, 1941. The lectotype has the locality data: Brazil, Amazonas, Tefé (Ega), IX.1921, A. H. Fassl leg. The specimen has served for the above mentioned figures (Schmidt's figures 4b and 7b) and it formerly has been lent to me for study (cf. Belle, 1963).

*Z. supratriangularis* is new to the fauna of Venezuela. If compared with the Brazilian examples of this species, the male from Venezuela is a darker specimen. The yellow markings along the ventral tergal margins of the abdominal segments 4 to 9 are much reduced and very narrow; they are well-developed and broad in the other examples. The superior caudal appendages are black for their proximal one-third; those of the male from Manaus are black at the extreme bases only. The caudal appendages (stylets) of the female from Manaus are entirely yellow.

The present males have three cubito-anal cross-veins (in addition to the inner side of the subtriangle) in the left fore wing, two in the

other wings. The female has two in each of its wings.

All wings have a traversing cross-vein in the supratriangle except for the left fore wing of the female which has none.

***Zonophora nobilis* spec. nov.**  
(figs. 57—66)

Material. — Brazil: Amazonas, Taracuá (Uaupes River), 14 August 1964, 1 ♂ (holotype), Machado & Pereira leg., CM.

This species is most nearly allied to *Z. supratriangularis* and it agrees with it in having the supratriangles traversed by a cross-vein. In the male sex it differs from *supratriangularis* in the following particulars:

(1) Superior caudal appendages almost three times as long as mid-dorsum of tenth abdominal segment; in *supratriangularis*, twice.

(2) Internal tooth of each superior caudal appendage at three-fifths the appendage's length; in *supratriangularis*, at half its length.

(3) Inferior lobe of anterior hamules long and slender; short and broad in *supratriangularis*.

(4) Inner margin of posterior hamules more strongly and more distally elbowed than in *supratriangularis*.

The female is unknown.

Male (holotype; much broken and missing some details such as labium, antennae, hairs of occipital crest, left posterior hamule, left superior caudal appendage). — Total length, 50 mm; abdomen, 40 mm (incl. caud. app., 3.1 mm); hind wing, 34 mm; costal edge of pterostigma in fore wing, 3.5 mm, in hind wing, 4.0 mm.

Face black, the following yellow: A medially interrupted stripe parallel to free border of labrum; a medially interrupted stripe on anteclypeus; and a complete cross-stripe on postclypeus covering fronto-clypeal suture. Mandibles externally yellow, the tips black. Superior surface of frons black except for two widely separated anterior spots of yellow. Vertex black, the conical prominences low. Occipital plate blackish brown, its posterior margin evenly concave. Rear of head black except for a brown median spot on occiput.

Prothorax dark brown, with mid-dorsal twin-spot of yellow and a larger yellow spot at either side. Pterothorax dark brown with yellow stripes; its colour design shaped as shown in the diagram.

Femora dark brown, the inner sides yellow.

Tibiae, tarsi and claws blackish brown.

Wings hyaline, the venation dark brown including frontal margin of costa. Pterostigma brown, surmounting 4½—5½ cells. Brace vein present. No basal subcostal cross-vein. Nodal index 12 : 19—19 : 10/12 : 14—14 : 12. Second primary antenodal cross-vein the eighth in fore wings, the seventh in hind wings. Intermedian cross-veins 8—7/5—4 in fore and hind wings, respectively. One extra cubito-anal cross-vein in each wing. Supratriangles and discoidal triangles two-celled. Subtriangles open. Hind wings with a three-celled anal triangle, six paranal cells, four postanal cells, and area posterior to Cu<sub>2</sub> four to five cells wide. Anal loop in hind wings open but small and not distinct, A<sub>2</sub> not angulated but curved.

Abdomen black with yellow markings as follows: Sides of 1 with large yellow marking; mid-dorsum of 2 with lanceolate yellow spot, the spot becoming wider at apex of segment, sides of 2 with large yellow marking interrupted by black behind auricle, margin of auricles black; sides of 3 with yellow marking bordering on whole ventral tergal margin, the marking being enlarged just in front of supplementary transverse carina; sides of 4 to 6 with yellow marking reaching to supplementary transverse carina, the markings becoming smaller on 4, 5 and 6 successively; basal half of 7 yellow, the yellow marking continued along ventral tergal margin, the supplementary transverse carinae black; sides of 8 with yellow basal marking, the marking continued along ventral tergal margin; segments 9 and 10 black. Superior caudal appendages pale yellow, becoming dark brown at both ends. Inferior caudal appendage black. Genital hamules and vesicle black. Caudal appendages and accessory genitalia shaped as shown in accompanying figures.

THE SPECIES IN THE MIMEOGRAPHED LIST OF  
RÁCENIS

Rácenis, in his mimeographed list of 1966, recorded four species of *Zonophora* from Venezuela. Three are indicated to be new and of these, two have been named (*cruxenti* and *medinali*). It is impossible to make out from the list which known species must be associated with these two names since Rácenis did not discuss them. Mr. De Marmels wrote to me on July 29, 1981: "I have almost all of his (Rácenis) handwritten manuscript notes, which later were published (or not), and also his collection catalogue. I can easily see what name he thought to put to which

Table 1. Distribution of *Zonophora* species and subspecies

Species and subspecies

	Argentina	Bolivia	Brazil	Ecuador	French Guyana	Guyana (Br.)	Paraguay	Peru	Surinam	Venezuela
<i>batesi</i> Selys		x		x	x			x		
<i>calippus calippus</i> Selys		x			x			x	x	x
<i>calippus klugi</i> Schmidt		x	x				x			
<i>calippus spectabilis</i> Campion	x	x				x				
<i>campanulata annulata</i> subsp. nov.			x							
<i>campanulata campanulata</i> (Burmeister)			x							
<i>campanulata machadoi</i> St. Quentin			x							
<i>diversa</i> spec. nov.	x		x				x			
<i>nobilis</i> spec. nov.			x							
<i>regalis</i> Belle									x	
<i>solitaria obscura</i> Belle								x		
<i>solitaria solitaria</i> Rácenis								x		
<i>supratriangularis</i> Schmidt			x						x	
<i>surinamensis</i> Needham			x							x
<i>wucherpfennigi</i> Schmidt			x							

species... *medinai* in the list became *solitaria* when published, and *cruxenti* in the collection catalogue became *regalis* Belle. He himself corrected the names in his catalogue."

The mimeographed list seems to have been composed for own use although copies of it have been distributed among some workers. The list has been mentioned in a dedication article of Dr. Janis Rácenis by De Marmels (1980) but it is difficult to believe that it must be considered an official publication.

#### HABITAT AND BEHAVIOUR IN THE FIELD

There is hardly any environmental and behavioural information available about *Zonophora* species. My experiences with regard to *Zonophora* have been confined to the two species *batesi* and *calippus calippus* only. I found them at the small shady creeks of the gallery forests in the savannah zone of Surinam. They were never encountered near stagnant water and also never during my collecting trips along the large streams of Surinam. For notes on their behaviour in the field reference is made to the paper by Belle (1963: 65, 67).

#### GEOGRAPHIC DISTRIBUTION

The genus *Zonophora* is limited in its geographic distribution to the Neotropical Region with the greatest number of species in Brazil (table 1). The most favourable habitat is apparently the tropical rainforest.

The type localities of the 15 species and subspecies are grouped as follows: Brazil 11, Venezuela 3, Paraguay and Peru each 1 (see table 2).

The *campanulata* group (fig. 67). The range of this group covers the southern part of Brazil and Paraguay, and the north-eastern part of Argentina. These parts do not fall within the area of the tropical rainforest.

The *calippus* group (fig. 68). This group has the largest range of all *Zonophora* groups. Its range extends from the northern coast of the continent to the southern part of Paraguay. The ranges of the members of the *calippus* group do not seem to overlap each other.

The *batesi* group (fig. 69). The two members of this group are primarily Amazonian in their distribution but *Z. batesi* also occurs along the northern coast of the continent.

The *supratriangularis* group (fig. 70). This group is not merely Amazonian in its distribution. *Z. supratriangularis* is also recorded from the Orinoco River in Venezuela (San Fernando de Atabapo).

The *surinamensis* group (fig. 71). Till now, all members of this group have been collected in the northern coastal region of the continent but the range may be larger.

In Rapoport's paper of 1968, continental South America has been divided into two sub-regions, Guayano-Brasileña and Andino-Patagonica. The distribution of the genus *Zonophora* lies within the sub-region Guayano-Brasile-

ñá. Using the zoogeographic division of continental South America after Sclater & Sclater (cf. Rapoport, 1968: 68) we can say that the members of the *campanulata* group occur in the Sud-brasileño region, the *batesi* group and *calippus* group mainly in the Amazónica region, and that both groups penetrate into the Colombiana region as far as the northern coast (Venezuela and the Guyanas), while the latter group also penetrates into the western part of the Sud-brasileño region. The *supratriangularis* group occurs mainly in the Amazónica region and the *surinamensis* group in the Colombiana region. The two cordilleras in the north-west of the continent seem to form a natural barrier for the distribution of *Zonophora* to the tropical rainforest of western Colombia and Central-America.

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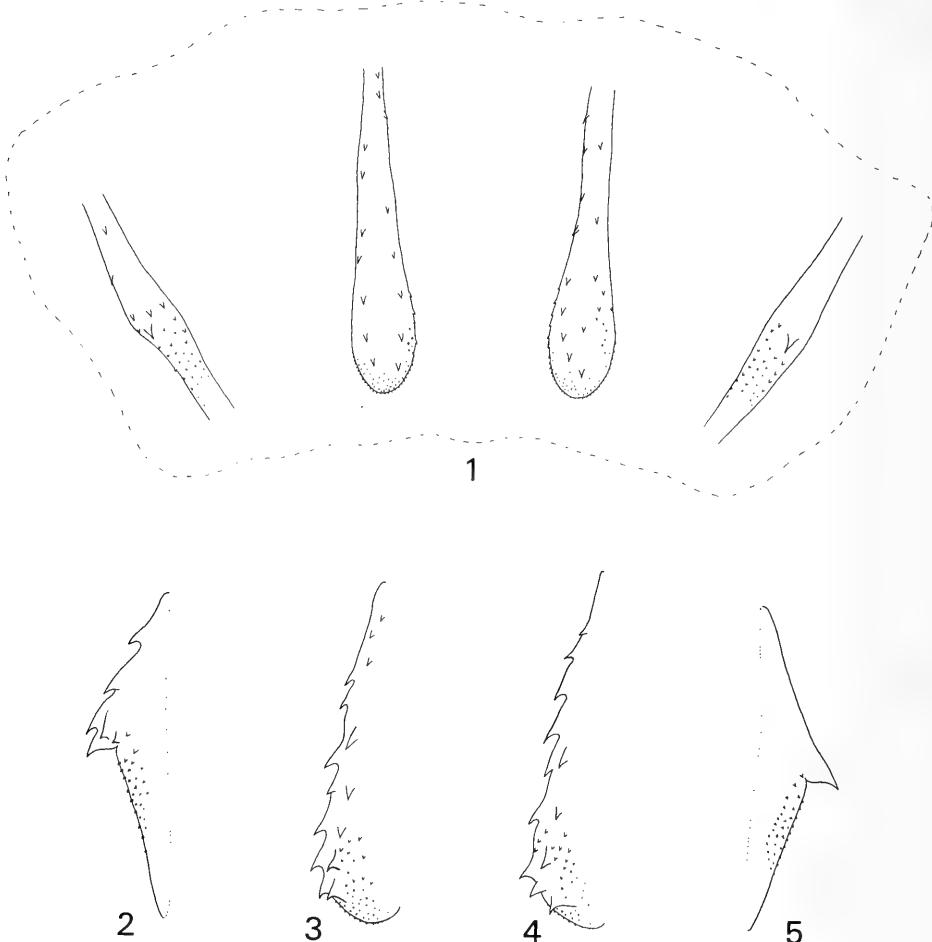
Table 2. Alphabetic list of the species and subspecies of *Zonophora*, with type localities, type status and type location.

Species and subspecies	Type locality	Type (all males) holo lecto neo	location
<i>batesi</i> Selys	Fonte Boa, Amazonas <sup>1)</sup> , Brazil	x	IRSN
<i>calippus calippus</i> Selys	Santarém, Pará, Brazil	x	IRSN
<i>calippus klugi</i> Schmidt	Mishiyacu, Peru		SMF
<i>calippus spectabilis</i> Campion	Sapucay, Paraguay	x	BM
<i>campanulata annulata</i> subsp. nov.	Jataí, Goiás, Brazil	x	MP
<i>campanulata campanulata</i> (Burmeister)	"Brazil"	lost	IRSN
<i>campanulata machadoi</i> St. Quentin	Serra do Cipo, Minas Gerais, Brazil	x	CM
<i>diversa</i> spec. nov.	Nova Teutonia, Santa Catarina, Brazil	x	CC <sup>2)</sup>
<i>nobilis</i> spec. nov.	Taracuá, Amazonas, Brazil	x	CM
<i>regalis</i> Belle	La Ceiba del Ventuari, Venezuela	x	IZM
<i>solitaria obscura</i> Belle	Sta. Elena, Venezuela	x	IZM
<i>solitaria solitaria</i> Rácenis	Guayaraca-Auyantepui, Venezuela	x	IZM
<i>supratriangularis</i> Schmidt	Tefé, Amazonas, Brazil		SMF
<i>surinamensis</i> Needham	Mapaoni, Território do Amapá, Brazil	x	CU
<i>wucherpfennigi</i> Schmidt	Manicoré, Amazonas, Brazil	x	CA <sup>3)</sup>

<sup>1)</sup> Because of practical reasons the states have been quoted following the locality names in Brazil.

<sup>2)</sup> Will be deposited in the National Museum of Natural History, Washington, D.C.

<sup>3)</sup> Collection Asahina, Tokyo.



Figs. 1—5. *Zonophora batesi* Selys, larva: 1, proventriculus; 2, first (left) dental fold, seen in oblique direction from right; 3, second dental fold, the same; 4, third dental fold, the same; 5, fourth dental fold, seen in oblique direction from left.

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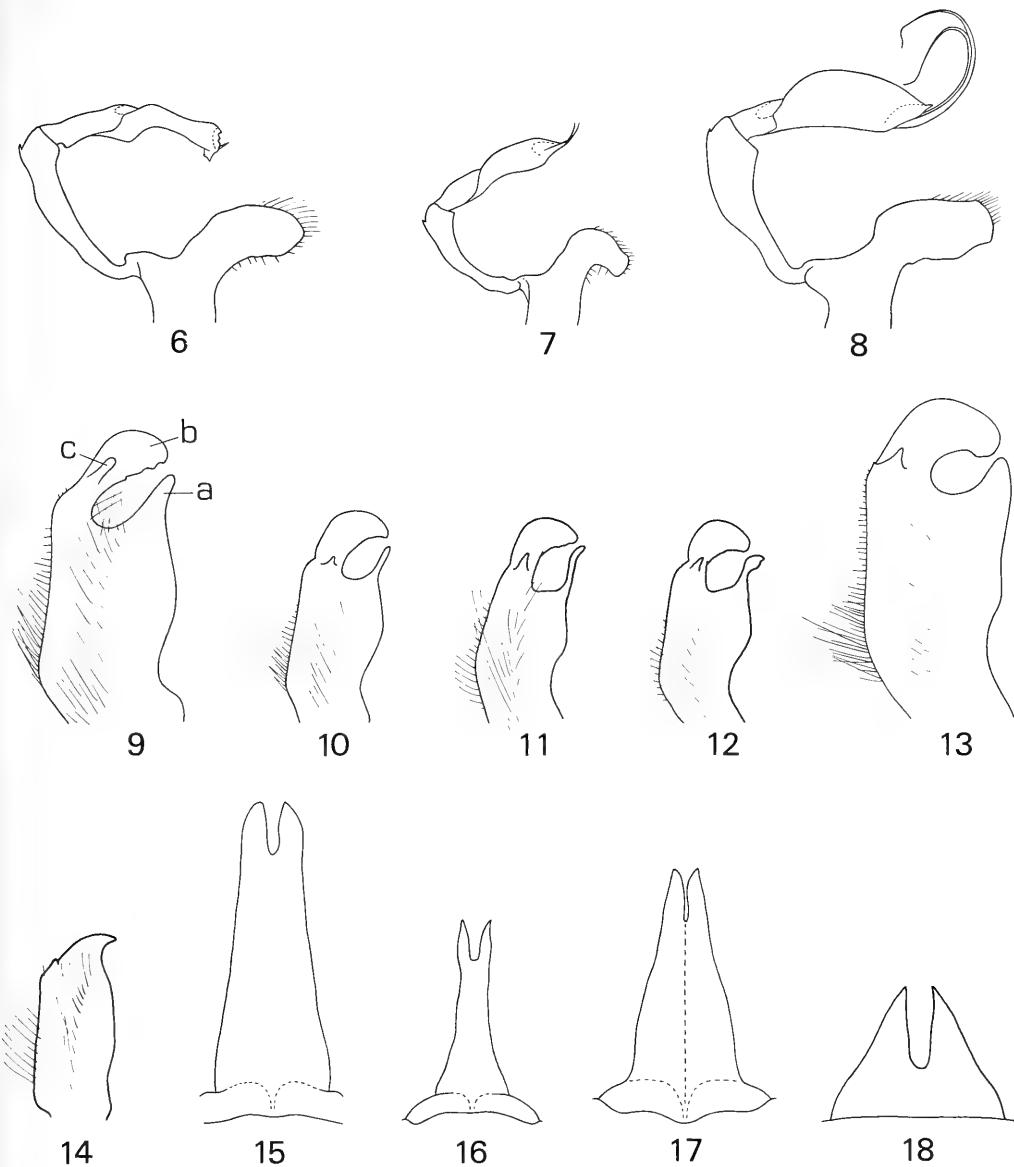
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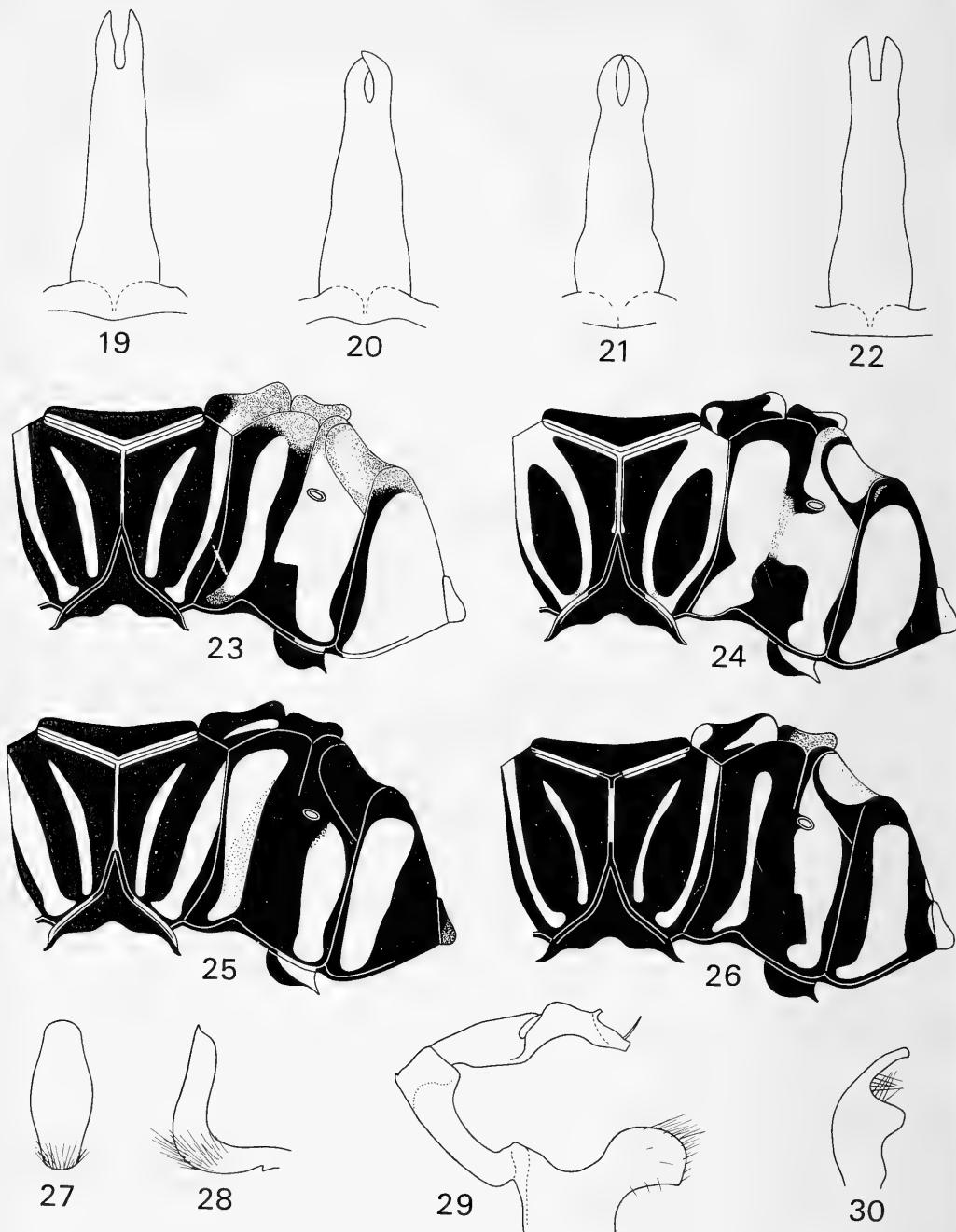
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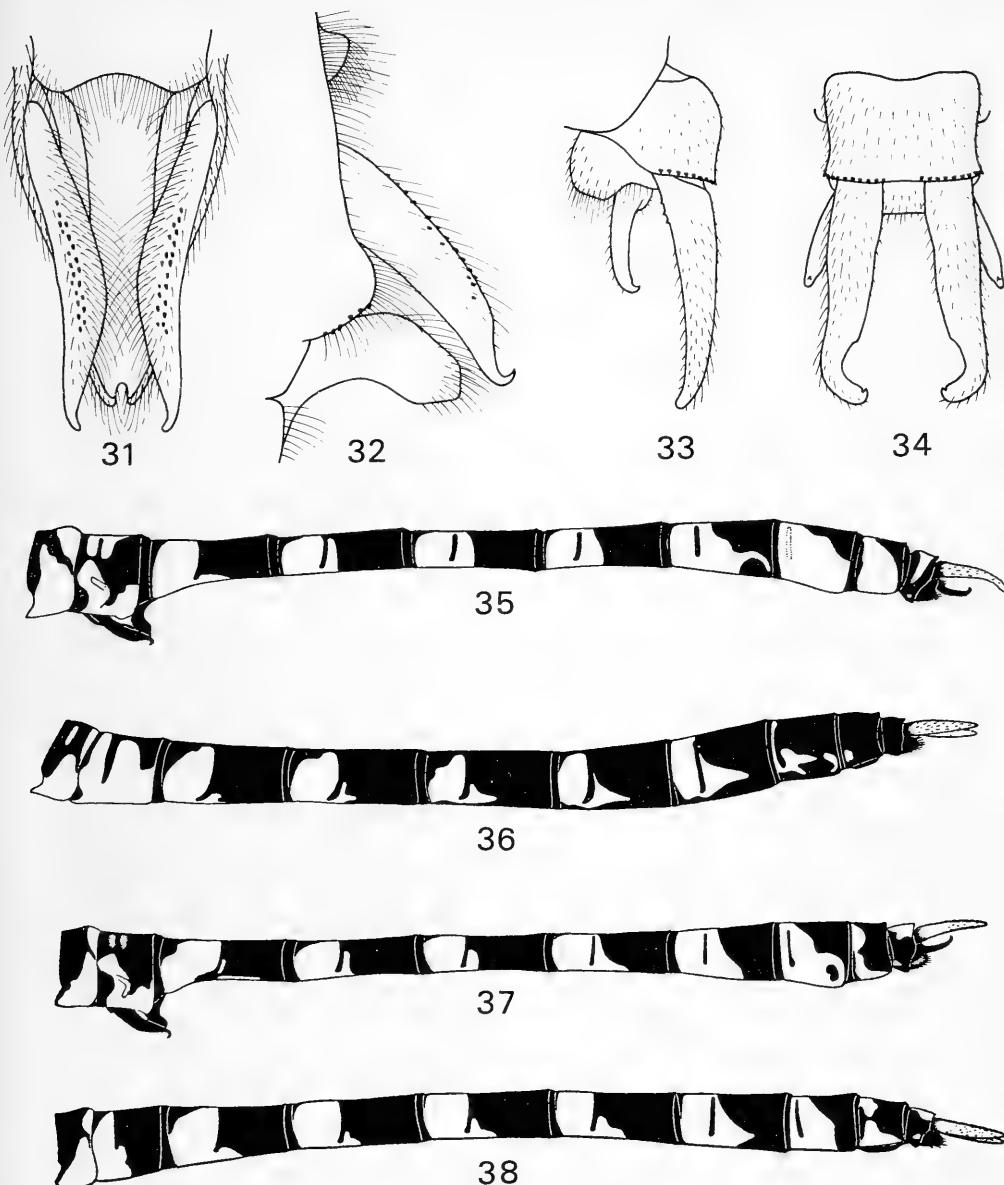
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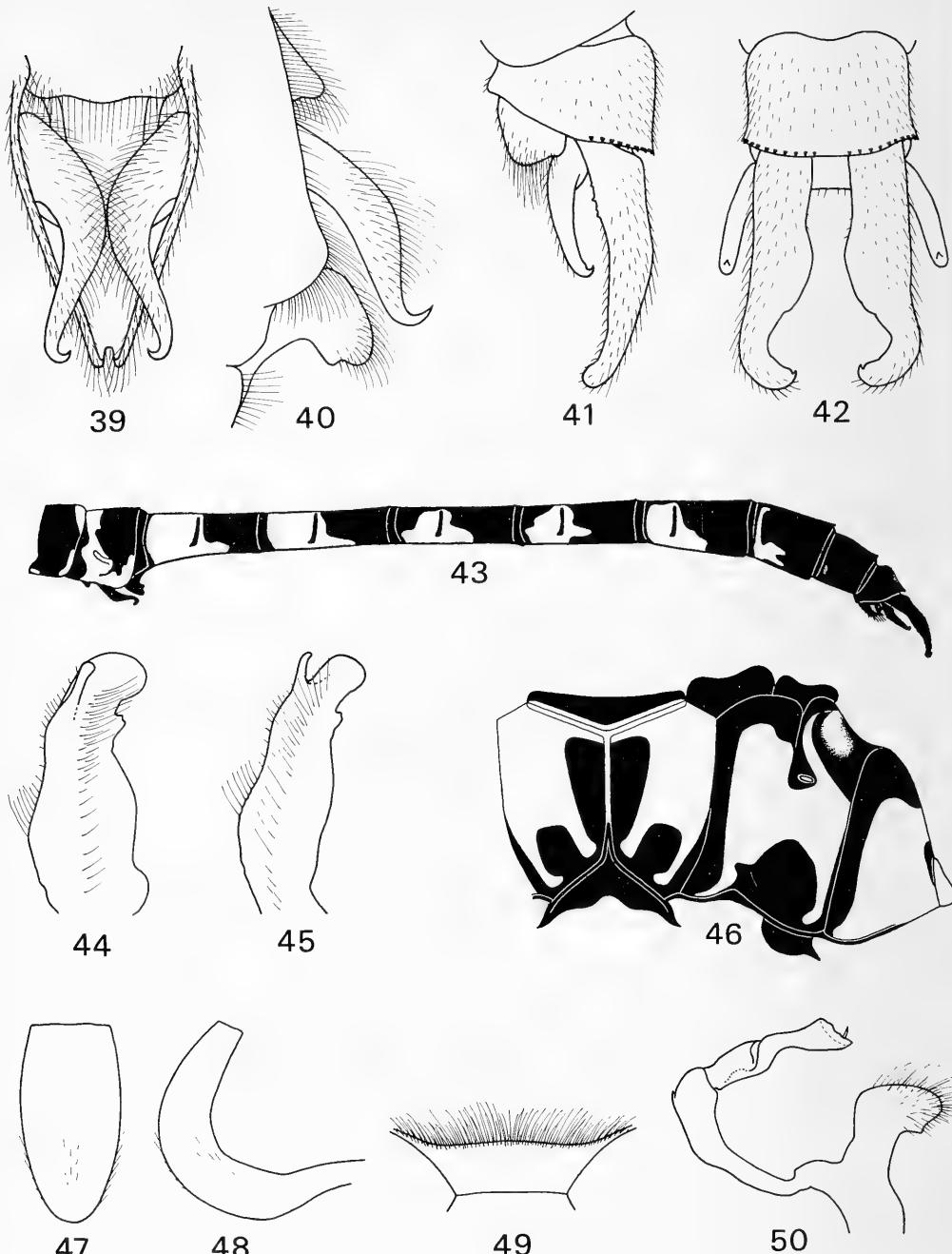
Figs. 6—8. Penes of *Zonophora*, right lateral view: 6, *Z. campanulata campanulata* (Burmeister); 7, *Z. calippus calippus* Selys; 8, *Z. batesi* Selys. Figs. 9—14. Left anterior hamules of *Zonophora*, right lateral view, showing superior lobe (a), inferior lobe (b), and internal lobe (c): 9, *Z. campanulata campanulata* (Burmeister); 10, *Z. calippus calippus* Selys; 11, *Z. calippus klugi* Schmidt; 12, *Z. calippus spectabilis* Campion; 13, *Z. batesi* Selys; 14, *Z. supratriangularis* Schmidt (more enlarged). Figs. 15—18. Vulvar laminæ of *Zonophora*, ventral view: 15, *Z. campanulata campanulata* (Burmeister); 16, *Z. calippus calippus* Selys; 17, *Z. batesi* Selys; 18, *Z. solitaria obscura* Belle, first described female.



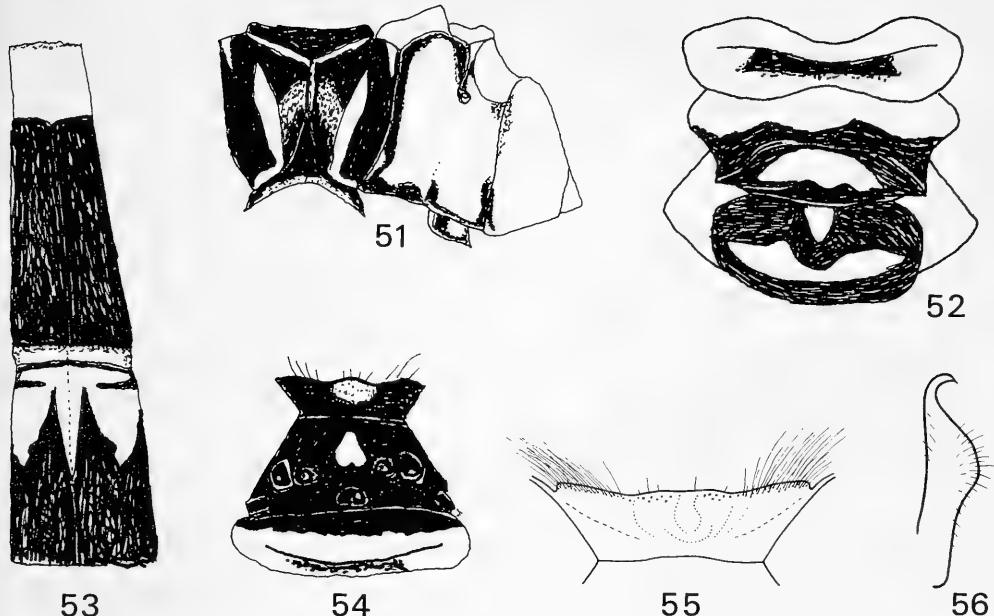
Figs. 19—22. Vulvar laminae of *Zonophora*, ventral view, showing variability: 19 and 20, *Z. campanulata campanulata* (Burmeister); 21, *Z. campanulata machadoi* St. Quentin, first described female; 22, *Z. campanulata annulata* subsp. nov., female allotype. Figs. 23—25. Diagram of thoracic colour pattern of *Zonophora*: 23, *Z. campanulata campanulata* (Burmeister); 24, *Z. campanulata machadoi* St. Quentin, male holotype; 25, *Z. campanulata annulata* subsp. nov., male holotype. Figs. 26—30. *Zonophora surinamensis* Needham, male: 26, diagram of thoracic colour pattern; 27, penis guard, frontal view; 28, the same, right lateral view; 29, penis, right lateral view; 30, left anterior hamule, right lateral view.



Figs. 31—34. *Zonophora campanulata campanulata* (Burmeister), male: 31, accessory genitalia (penis and penis guard not drawn), ventral view; 32, same, right lateral view; 33, tenth abdominal segment and caudal appendages, left lateral view; 34, the same, dorsal view. Figs. 35—36. *Zonophora campanulata machadoi* St. Quentin, left lateral view of abdomen: 35, male holotype; 36, first described female. Figs. 37—38. *Zonophora campanulata annulata* subsp. nov., left lateral view of abdomen: 37, male holotype; 38, female allotype.

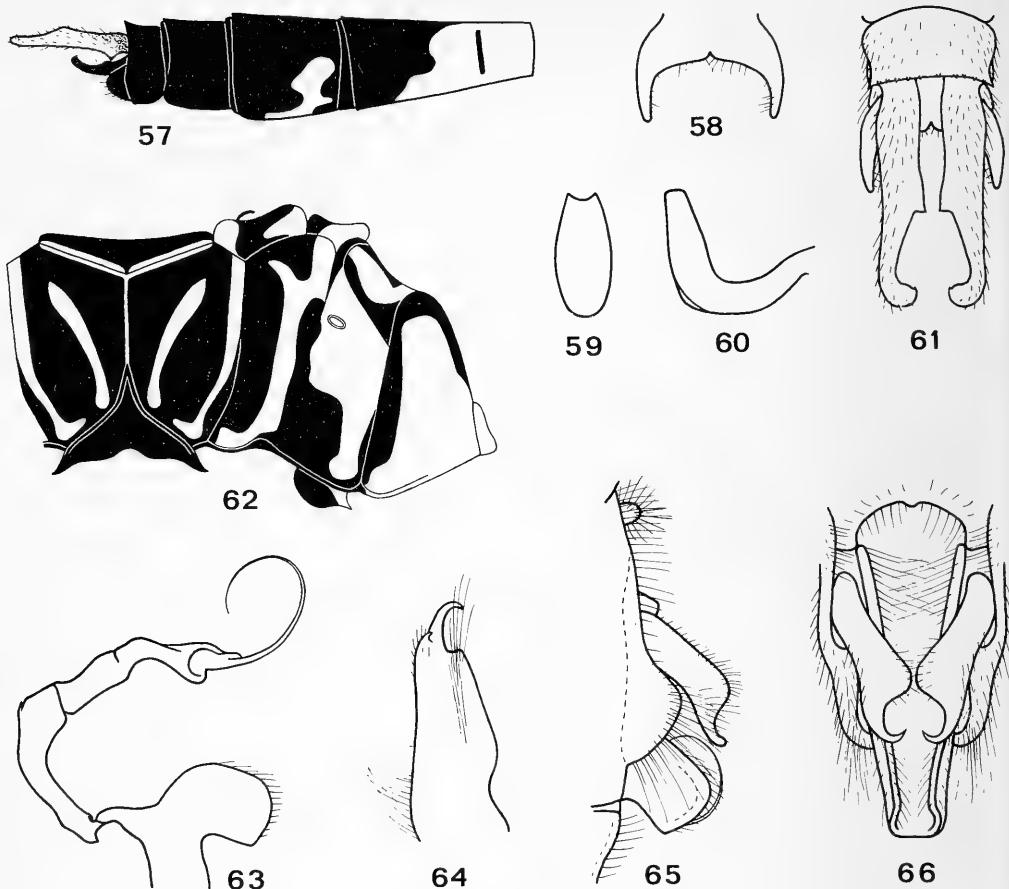


Figs. 39—50. *Zonophora diversa* spec. nov., male holotype: 39, accessory genitalia (penis and penis guard not drawn), ventral view; 40, the same, right lateral view; 41, tenth abdominal segment and caudal appendages, left lateral view; 42, the same, dorsal view; 43, abdomen, left lateral view; 44, left anterior hamule, right lateral view; 45, the same, seen in oblique direction from right; 46, diagram of thoracic colour pattern; 47, penis guard, frontal view; 48, the same, right lateral view; 49, occipital plate; 50, penis, right lateral view.



Figs. 51—54. *Zonophora solitaria solitaria* Rácenis, male holotype: 51, diagram of thoracic colour pattern; 52, face and frons, seen in oblique direction from front; 53, abdominal segments 7 and 8, dorsal view; 54, frons, vertex and occipital plate. (Figs. 51—54, after J. de Marmels, June 1981.) Fig. 55. *Zonophora solitaria obscura* Belle, first described female: Occipital plate. Fig. 56. *Zonophora supratriangularis* Schmidt: Left posterior hamule, ventral view.

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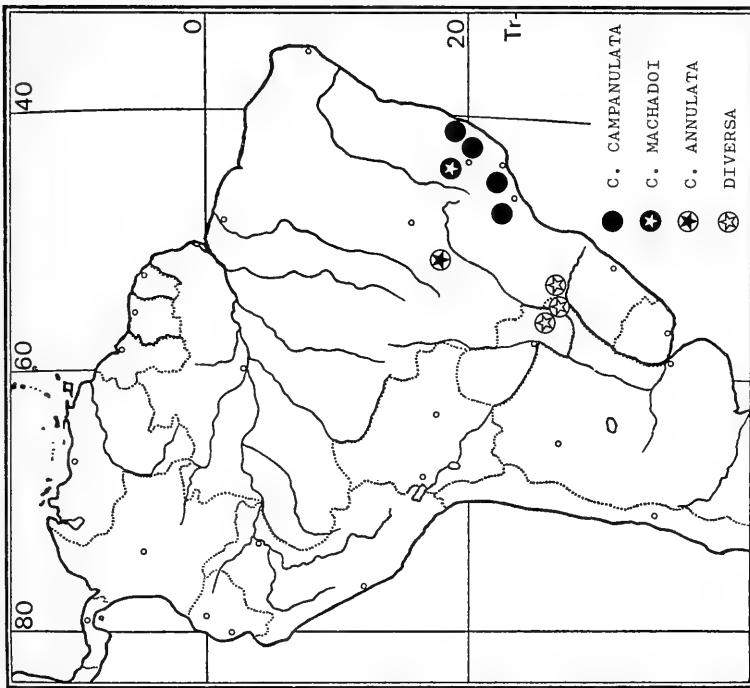
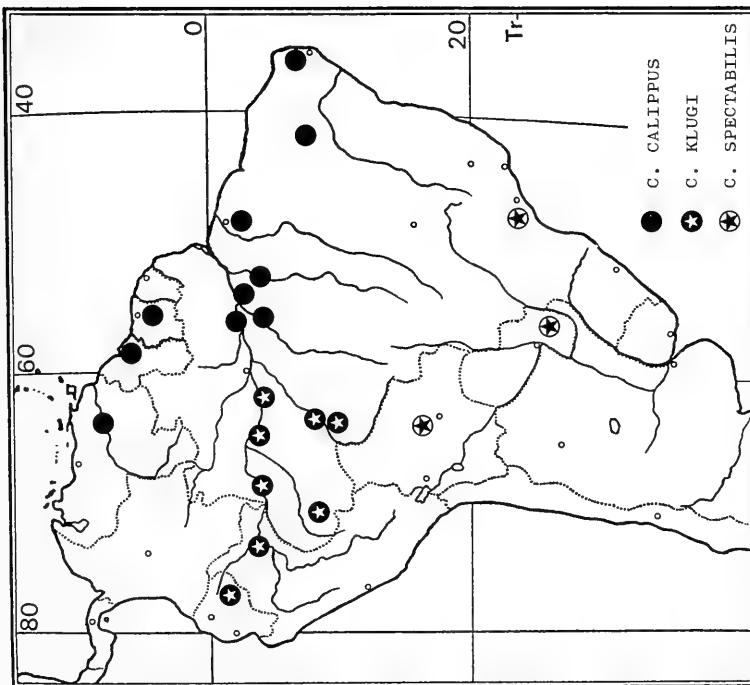
Figs. 57—66. *Zonophora nobilis* spec. nov., male holotype: 57, apical segments of abdomen, right lateral view; 58, inferior caudal appendage, dorsal view; 59, penis guard, frontal view; 60, the same, right lateral view; 61, tenth abdominal segment and caudal appendages, dorsal view; 62, diagram of thoracic colour pattern; 63, penis, right lateral view; 64, left anterior hamule, right lateral view; 65, accessory genitalia, right lateral view; 66, the same, ventral view.

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Fig. 67. Distribution of the *campanulata* group.Fig. 68. Distribution of the *calippus* group.

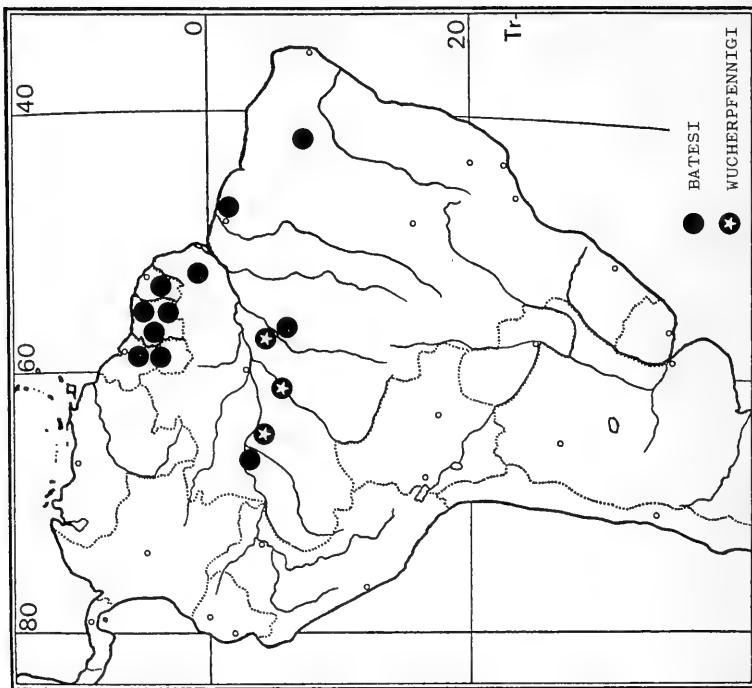


Fig. 69. Distribution of the *batesi* group.

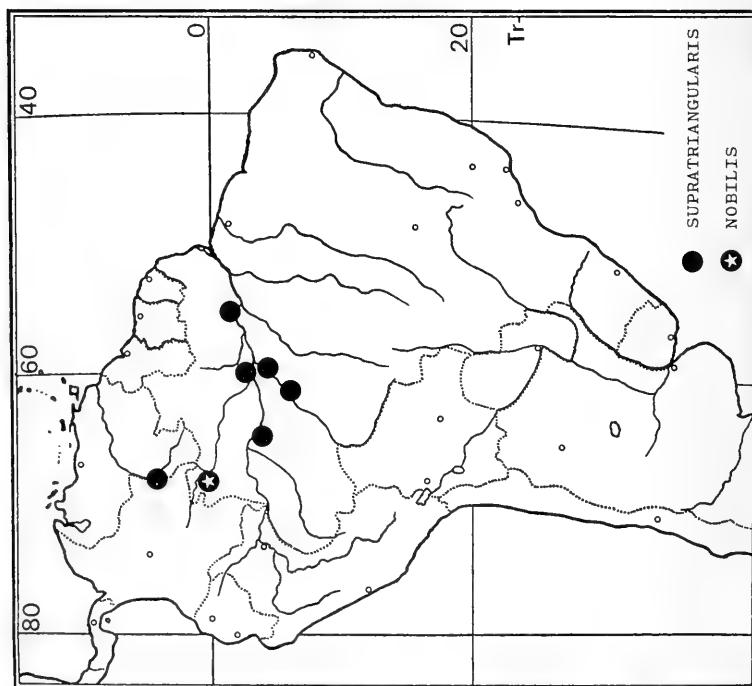


Fig. 70. Distribution of the *supratriangularis* group.

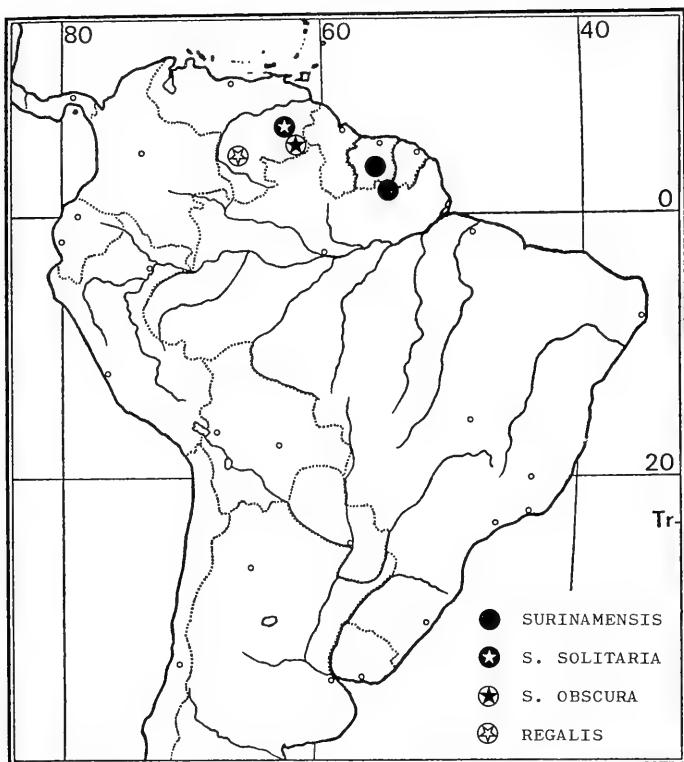
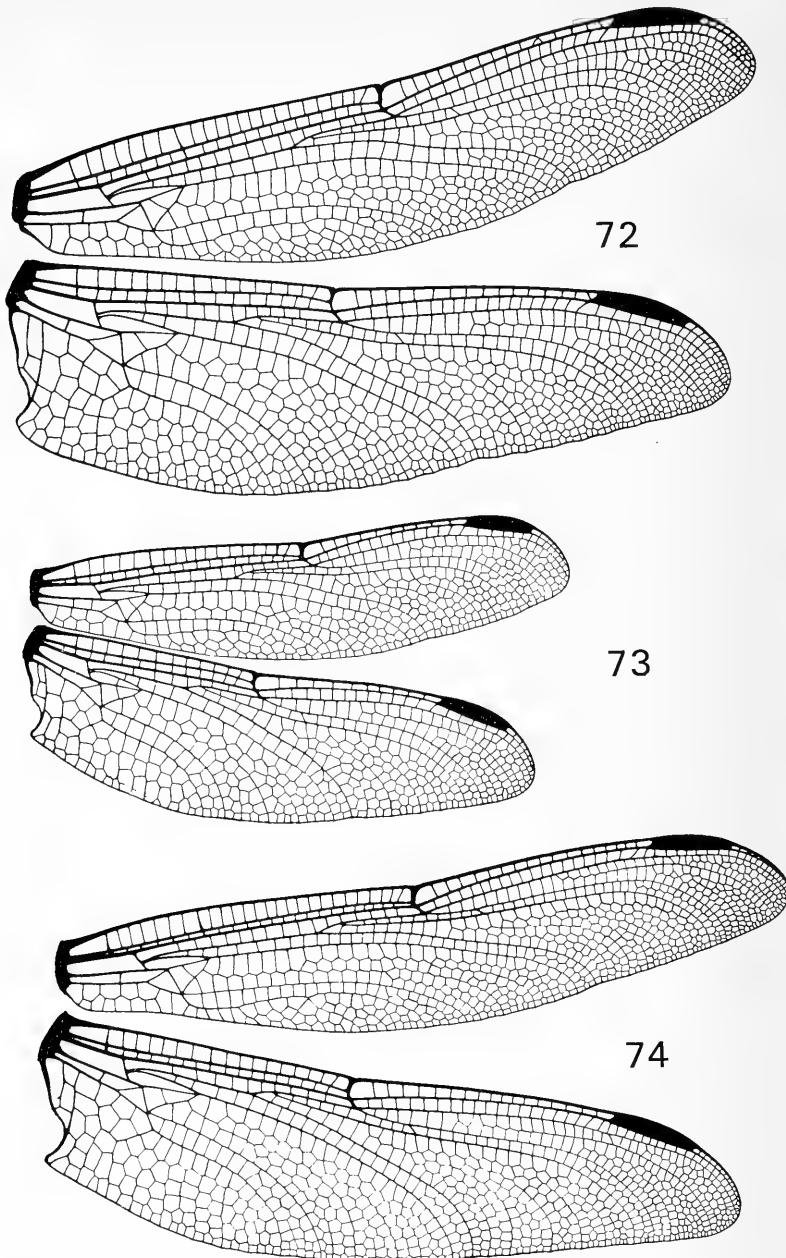
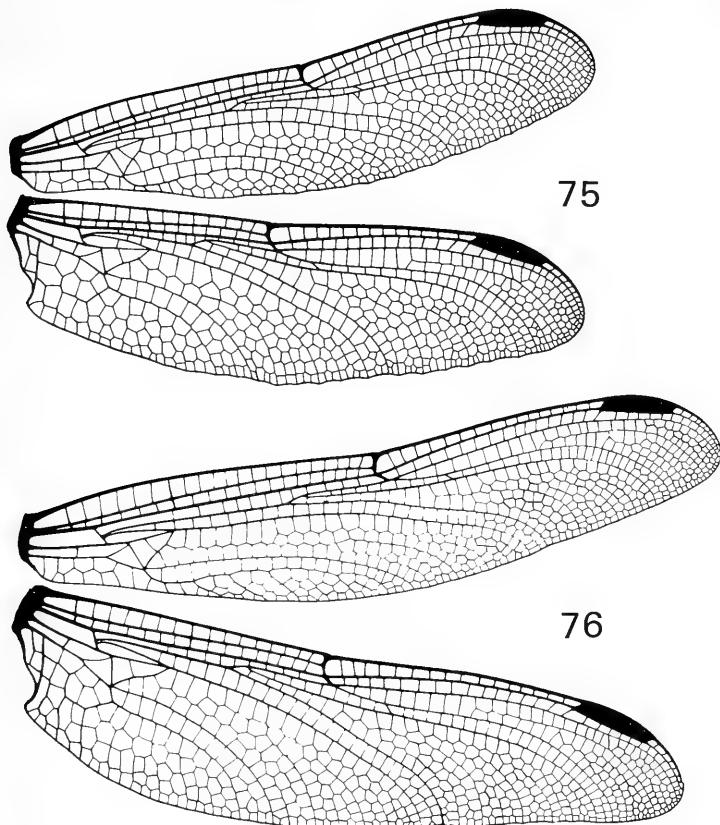


Fig. 71. Distribution of the *surinamensis* group.



Figs. 72—74. Right pair of wings of male: 72, *Zonophora campanulata campanulata* (Burmeister); 73, *Zonophora calippus calippus* Selys; 74, *Zonophora batesi* Selys.



Figs. 75—76. Right pair of wings of male: 75, *Zonophora supratriangularis* Schmidt; 76, *Zonophora surinamensis* Needman.







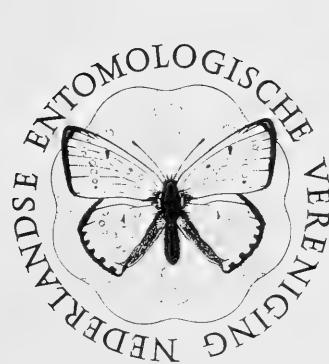




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## INHOUD

C. VAN ACHTERBERG. — Six new genera of Braconinae from the Afrotropical Region (Hymenoptera, Braconidae), pp. 175—202, figs. 1—147.



# SIX NEW GENERA OF BRACONINAE FROM THE AFROTROPICAL REGION (HYMENOPTERA, BRACONIDAE)

by

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Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands

## ABSTRACT

The new tribe Adeshini is defined for the genera *Adesha* Cameron, 1912, and *Adeshoides* gen. nov. (type-species: *A. asulcatus* sp. nov. from Senegal). The genera with a facial protuberance in the Braconinae (excluding the *Atanycolus* group with petiolate pedicellus) are keyed and (re)described. Three new genera from the Afrotropical region are described, viz., *Malagopsis* (type-species: *Plaxopsis grandidieri* Szépligeti, 1913), *Deltaphyma* (type-species: *D. horstoki* sp. nov. from South Africa), and *Zanzopsis* (type-species: *Plaxopsis liogaster* Szépligeti, 1913). *Bracon nigriceps* Brullé, 1846, is a new junior synonym of *Lasiophorus lanceolator* (Fabricius, 1804) and *Lasiophorus seyrigi* Granger, 1949, is synonymized with *Malagopsis grandidieri* (Szépligeti, 1913) comb. et syn. nov. The genus *Plaxopsis* Szépligeti, 1905, is removed from the synonymy with *Lasiophorus* Haliday, 1833, and a lectotype is designated for *Lasiophorus seyrigi* Granger, 1949, and *Plesiobracon carinatus* Cameron, 1903. Finally the *Plesiobracon* group is defined, the known genera are keyed and two new genera are described: *Carinibracon* (type-species: *C. danielsoni* sp. nov. from Senegal) and *Kenema* (type-species: *K. quickei* sp. nov. from Sierra Leone). *Odontogaster* Szépligeti, 1906, is a new junior synonym of *Soter* Saussure, 1892.

In this paper some recently discovered new genera of the Braconinae from the Afrotropical region are described, illustrated and keyed. Among these are two new genera collected during the Gambia-Senegal Expedition of the Lund University in 1977, kindly sent on loan by Dr. R. Danielsson (Lund). Both new genera have a sistergroup in the Oriental region as far as can be deduced from our limited knowledge of the genera of Braconidae. Dr. D. Quicke (Nottingham) kindly allowed me to describe a related new genus from Sierra Leone.

During my visits to the Berlin Museum (1979, 1982) I found several genera from the Afrotropical region which at present are included in the genus *Plaxopsis*. These genera are (re)described in this paper, together with a new genus from South Africa found in the collection of the Rijksmuseum van Natuurlijke Historie at Leiden. For the terminology used in this paper, see Van Achterberg, 1979: 242—249.

## ADESHINI tribus nov.

**Diagnosis.** — Contains the only known Braconinae with vein CU1a of fore wing at same level as vein 2-CU1 (fig. 4) and vein CU1b of fore wing much longer than vein 3-CU1 (a synapomorphy within the Braconinae); scapus

truncate apically (fig. 3); mesoscutum at least sparsely setose; vein r-m of hind wing very short (fig. 4); propodeum with complete longitudinal carina (fig. 11); 1st tergite movably connected to 2nd tergite; 2nd and 3rd metasomal tergites with no antero-lateral diverging grooves (fig. 1).

Contains two genera: *Adesha* Cameron, 1912 (Oriental region) and *Adeshoides* gen. nov. (Afrotropical region). The biology is unknown.

## KEY TO GENERA OF THE TRIBE ADESHINI NOV.

1. Mesoscutum with deep medio-posterior groove (fig. 146); laterope large and round (fig. 139); angle between veins 1-SR and C+SC+R of fore wing about 35° (fig. 140); head and mesosoma smooth; mesoscutum densely setose ..... *Adesha* Cameron
- Mesoscutum without medio-posterior groove (fig. 11); laterope (virtually) absent (fig. 1); angle between veins 1-SR and C+SC+R of fore wing about 65° (fig. 7); head and mesosoma coriaceous; mesoscutum sparsely setose, mainly near the notauli ..... *Adeshoides* gen. nov.

## *Adeshoides* gen. nov.

Type-species: *Adeshoides asulcatus* sp. nov.

**Etymology:** Latin for resembling the genus *Adesha*. **Gender:** masculine.

**Diagnosis.** — Head and mesosoma coriaceous; scapus rather robust (fig. 3); apex of antenna with no spine (fig. 5); eyes glabrous and not emarginate (fig. 9); malar suture absent; mesoscutum sparsely setose (mainly near the notaui) and without medio-posterior depression (fig. 11); pleural and mesosternal sutures smooth; antescutal depression virtually absent (fig. 1); metapleural flange absent; only anterior half of notaui impressed; scutellar sulcus narrow (fig. 11); metanotum medially with weak longitudinal carina (fig. 11); propodeal spiracle round, situated submedially (fig. 1); angle between veins 1-SR and C-SC+R of fore wing about 65° (fig. 7); vein 1-SR+M of fore wing straight; vein m-cu of fore wing far antefurcal and distinctly diverging from vein 1-M posteriorly (fig. 4); vein 1-R1 of fore wing much longer than pterostigma (fig. 4); hind wing setose basally; tarsal claws setose, with no lobe (fig. 6); ventral row of setae of hind tarsus indistinct; laterope (virtually) absent (fig. 1); dorso-lateral and dorsal (except basally: fig. 12) carinae of 1st tergite present; 2nd metasomal suture deep and smooth (fig. 12); 2nd tergite with no medio-basal area, with a weak medial carina and a pair of shallow parallel, sublateral grooves (fig. 12); 2nd-5th metasomal segments with no antero-lateral grooves and with distinct sharp lateral crease (fig. 1).

**Distribution.** — Afrotropical: one species.

***Adeshoides asulcatus* sp. nov.**  
(figs. 1—12)

Holotype, ♂, length of body 2.5 mm, of fore wing 2.2 mm.

**Head.** — Antennal segments 37, length of 3rd segment 1.3 times 4th segment, length of 3rd and 4th segments 2.7 and 2.0 times their width, respectively; penultimate segment of antenna 2× longer than wide (fig. 5); length of maxillary palp 0.7 times height of head; length of eye in dorsal view 2.8 times temple (fig. 8); temples gradually narrowed posteriorly; POL : Ø ocellus : OOL = 5 : 4 : 10; frons weakly convex, coriaceous, with weak medial groove; face and clypeus rather convex and shiny coriaceous; ventral margin of clypeus not differentiated; length of malar space 0.8 times basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.4 times its height; episternal scrobe linear and rather shallow; mesoscutal lobes and scutellum rather

flat and coriaceous; posterior face of propodeum rather differentiated and shorter than anterior face.

**Wings.** — Fore wing: r : 3-SR : SR1 = 5 : 13 : 35; veins M+CU1, CU1, r, 3-SR, SR1 and 2-M distinctly wider than other veins; cu-a interstitial; 2-SR : 3-SR : r-m = 7 : 13 : 6.

**Legs.** — Hind coxa smooth; length of femur, tibia and basitarsus of hind leg 4.6, 10.4, and 7 times their width, respectively; hind tibial spurs both 0.2 times hind basitarsus.

**Metasoma.** — Length of 1st tergite 0.8 times its apical width, its surface largely rugulose-coriaceous; dorsal carinae of 1st tergite nearly complete, but rather weak and not lamelliform (fig. 12); 2nd tergite coriaceous-rugulose; 3rd and 4th tergites shiny coriaceous; rest of metasoma smooth and depressed; 4th and 5th tergites with smooth, deep anterior transverse groove (fig. 1).

**Colour.** — Brownish-yellow; apical half of antenna and stemmaticum, dark brown; pterostigma and veins (rather dark) brown; wing membrane slightly infuscated.

Holotype in Entomological Museum, Lund: "Senegal, 3 km SSW Toubakouta, 10 km S Ziguinchor, 4.iii.1977, at light 19.00—22.00, Loc. No. 16, UTM 28PCJ 58 782", "Lund Univ. Syst. Dept. Sweden, Gambia/Senegal, Febr.-March 1977, Cederholm, Danielsson, Larsson, Mireström, Norling, Samuelson".

***Adesha* Cameron, 1912**  
Cameron, 1912: 78; Shenefelt, 1978: 1430.

Type-species: *Adesha albolineata* Cameron, 1912 (monotypic). **Gender:** feminine.

**Diagnosis.** — Head and metasoma smooth; scapus rather robust (fig. 138); eyes glabrous and indistinctly emarginate (fig. 142); malar suture absent; mesoscutum densely setose and with deep medio-posterior groove (fig. 146); pleural and mesosternal sutures smooth; antescutal depression very narrow; metapleural flange small (fig. 139); anterior half of notaui deep and smooth, rest shallow or absent (fig. 146); scutellar sulcus wide and distinctly crenulate (fig. 146); metanotum with distinct medio-longitudinal carina (fig. 146); propodeal spiracle rather small, round, and behind middle of propodeum (fig. 139); angle between veins 1-SR and C+SR+R of fore wing about 35° (fig. 140); vein 1-SR+M of fore wing straight; vein m-cu of fore wing moderately antefurcal

and slightly diverging posteriorly from vein 1-M (fig. 141); tarsal claws setose, without lobe (fig. 143); ventral row of setae of hind tarsus distinct; laterope large and round (fig. 139); dorso-lateral carinae of 1st tergite distinct; dorsal carinae on basal quarter of tergite, rest absent (fig. 147); 2nd metasomal suture deep and crenulate (fig. 147); 2nd tergite with narrow triangular and smooth medio-basal area, bordered by crenulate grooves, laterally with a pair of posteriorly (weakly) converging depressions (fig. 147); 2nd-5th tergites with sharp lateral crease and without antero-lateral grooves (fig. 139); ovipositor normal, with neither nodus nor teeth subapically.

Distribution. — Oriental: one species.

**Adesha albolineata** Cameron  
(figs. 138—147)

Cameron, 1912: 78; Shenefelt, 1978: 1431.

Holotype, ♀, length of body 4.2 mm, of fore wing 3.8 mm.

Head. — Antennal segments incomplete, 16 present, length of 3rd segment 1.5 times 4th segment, length of 3rd and 4th segments 3 and 2 times their width, respectively; length of maxillary palp 0.7 times height of head; length of eye in dorsal view 2.8 times temple; temples roundly narrowed posteriorly (fig. 145); POL : Ø ocellus : OOL = 7 : 8 : 19; frons slightly convex, largely smooth and with medial groove (fig. 142); face weakly convex and smooth; clypeus flat and smooth, its ventral margin not differentiated from clypeus, concave; length of malar space 0.8 times basal width of mandible.

Mesosoma. — Length of mesosoma 1.7 times its height; side of pronotum smooth, except for the finely crenulate medial groove; mesopleuron smooth; episternal scrobe deep, medium-sized and round (fig. 139); mesoscutum rather convex, its middle lobe slightly impressed medially (fig. 146); scutellum weakly convex and somewhat pimply; propodeum largely smooth, with some short rugae near medial carina and its posterior surface not differentiated (fig. 146).

Wings. — Fore wing: r : 3-SR : SR1 = 5 : 10 : 38; veins of similar width; 1-CU1 : 2-CU1 = 1 : 17; 2-SR : 3-SR : r-m = 10 : 10 : 7.

Legs. — Hind coxa smooth and slender (fig. 139); length of femur, tibia and basitarsus of hind leg 4.1, 9.8, and 6.4 times their width, respectively; length of hind tibial spurs 0.2 and 0.3 times hind basitarsus.

Metasoma. — Length of 1st tergite 0.8 times

its apical width, its surface coarsely reticulate medially, rest smooth (fig. 147); 3rd tergite coarsely reticulate medially, as rest of metasoma (fig. 139); length of ovipositor sheath 0.20 times fore wing, widened apically; hypopygium medium-sized and truncate apically.

Colour. — Brownish-yellow; antenna, dorsal part of head largely, meso- and metasoma dorsally, mesosternum partly, ovipositor sheath, tarsi, patch on apex of hind tibia, hind femur dorsally, dark brown or black; metasoma laterally, and apex of 5th tergite yellowish; wing veins and pterostigma brown; wing membrane subhyaline.

Holotype in British Museum (Natural History), London: "Type", "Kuching, J. H." (= John Hewitt), "2.10", "P. Cameron Coll., 1914-110", "Adesha albolineata Cam., Type, Borneo" (in Cameron's handwriting).

KEY TO THE GENERA OF THE BRACONINAE WITH FACIAL PROTUBERANCE (excluding the *Atanycolus* group)

1. Head with a protuberance anteriorly (figs. 13, 23, 35, 84); if rather cariniform and small, then in dorsal view (short) semi-circularly protruding; (some males of *Magalopsis grandidieri* (Szépligeti) have no protuberance but face is (narrowly) depressed medially) ..... 2
- Head without protuberance, at most clypeus with a scarcely protruding, medially straight (in dorsal view), fine, dorsal carina; (face without medio-dorsal depression) ..... other Braconinae
2. Pedicellus in dorsal view cylindrical, not narrowed basally; scapus rounded subbasally (figs. 17, 32); inner aspect of scapus not excavated apically (fig. 38), except in *Deltaphyma* (fig. 56); length of fore tarsus less than 1.7 times fore tibia ..... 3
- Pedicellus in dorsal view petiolate, distinctly narrowed basally; scapus rather angularly protruding subbasally; inner aspect of scapus deeply excavated medio-apically; length of fore tarsus 1.7—2 times fore tibia ..... *Atanycolus* group
3. Middle of face with an irregularly incised, vertical lamella (fig. 13); antenna of ♀ widened apically and with a blunt apex (figs. 13, 14); marginal cell of fore wing short, far removed from wing apex (fig. 15); vein 1-SR of fore wing short (fig. 15); tibial spurs dorsally glabrous and

- ventrally setose ..... *Victoroviella* Tobias
- Middle of face without vertical lamella (figs. 23, 58, 60); antenna of ♀ not widened apically and with acute apex (figs. 24, 41); marginal cell of fore wing long, almost reaching wing apex (figs. 31, 70); vein 1-SR of fore wing medium-sized (figs. 31, 42, 59); tibial spurs evenly setose or nearly completely glabrous (at 50 $\times$ ) ..... 4
4. Face with protruding carina and/or lamella (figs. 35, 52, 77); clypeus with ventral carina (figs. 49, 77); mesoscutum largely glabrous; hind spurs (partly) setose; medio-basal area of 2nd tergite robust (figs. 48, 65, 82); antero-lateral grooves of 3rd tergite (partly) crenulate (figs. 48, 93); (Afrotropical and South Palaearctic) ..... 5
- Face with robust horn above clypeus (figs. 23, 26 of type species, in other species spoon-shaped or tuberculiform); clypeus without distinct ventral carina (fig. 23); mesoscutum completely setose; hind spurs almost completely glabrous; medio-basal area of 2nd tergite very slender (fig. 34); antero-lateral grooves of 3rd tergite smooth; (Neotropical) ..... *Lasiophorus* Haliday
5. Upper half of face protruding (figs. 58, 75) or slightly concave (fig. 87); posterior half of 4th and 5th tergites flat (figs. 57, 84); 1st tergite usually without dorsal carinae (figs. 65, 82), if present then not lamelliform; vein 1r-m of hind wing straight (fig. 55); 2nd tergite with (sub)parallel depressions (figs. 65, 82, 93); vein 1-M of fore wing straight (figs. 55, 70, 91); 1st discal cell of fore wing less transverse (figs. 55, 91); lower facial protuberance of ♀ distinctly lamelliform or absent; (Continental Africa and South Palaearctical region) ... 6
- Upper half of face deeply concave (figs. 47, 49); posterior half of 4th and 5th tergites strongly convex (fig. 35); 1st tergite with lamelliform dorsal carinae (fig. 48); vein 1r-m of hind wing curved (fig. 39); 2nd tergite with (incomplete) diverging antero-lateral grooves (fig. 48); vein 1-M of fore wing somewhat bent posteriorly (fig. 42); 1st discal cell of fore wing comparatively transverse (fig. 39); lower facial protuberance of ♀ sublamelliform and absent in ♂ and exceptionally in (small) ♀♀ (Malagasy) ..... *Malagopsis* gen. nov.
6. Scapus truncate or at most moderately protruding ventrally, not beyond apex of pedicellus (figs. 69, 92); frons not or shallowly concave (figs. 74, 88); face with either a lamella (figs. 84, 87) or a W-shaped protuberance (figs. 75, 77); 2nd tergite with well-defined basal area (figs. 82, 93); 2nd tergite not projecting above 2nd suture (fig. 84); groove between eye and antennal socket rather shallow or absent (figs. 67, 84); mesoscutum anteriorly at least as high as the pronotum anteriorly (figs. 67, 84); scutellum often with a small pit (fig. 76) ..... 7
- Scapus strongly protruding ventro-apically, well beyond apex of pedicellus (fig. 54); frons distinctly concave (fig. 62); face with protruding lamella and with a triangular protuberance above it (figs. 58, 60); 2nd tergite with ill-defined basal area (fig. 65); 2nd tergite medio-posteriorly projecting above 2nd suture (fig. 52); with a deep groove between eye and antennal socket (fig. 52); mesoscutum anteriorly lower than pronotum anteriorly (fig. 52); scutellum without small pit (fig. 63) ..... *Deltaphyma* gen. nov.
7. Face above clypeus with W-shaped protuberance (figs. 75, 77); marginal cell of hind wing strongly narrowed apically (fig. 70) ..... *Zanzopsis* gen. nov.
- Face above clypeus without protuberance, only submedially with a more or less semi-circular (often minute) lamella (fig. 87); marginal cell of hind wing (sub)-parallel-sided or slightly narrowed apically (fig. 91) ..... *Plaxopsis* Szépligeti

### *Victoroviella* Tobias, 1975

Tobias, 1975: 962—964.

Type-species: *Victoroviella deserticola* Tobias, 1975.

Diagnosis. — Scapus slightly longer ventrally than dorsally (fig. 13), curved, with a rounded anterior flange (figs. 13, 17) and subcylindrical; antenna of ♀ widened and rather compressed apically (fig. 13); apex of antenna blunt (fig. 14); face with longitudinal thin lamella, which has one deep medial and some smaller incisions (fig. 13), below this lamella a spoon-shaped, weakly concave protuberance (fig. 18); notaui absent; scutellar sulcus rather shallow and narrow; metanotum without carinae; vein 1-R1 (metacarp) of fore wing much shorter than pterostigma (fig. 15); fringe of wings very short; basal half of fore wing only sparsely setose; parastigma comparatively robust (fig. 15);

vein r-m of hind wing very short (fig. 15); marginal cell of hind wing narrowed apically; tibial spurs dorsally glabrous and ventrally setose; tarsal claws large (fig. 20), setose, and with no lobe; dorsal and dorso-lateral carinae of 1st tergite absent; 2nd suture of metasoma deep, smooth and straight (fig. 21); 2nd and basal half of 3rd tergite with sharp lateral crease; 2nd and 3rd tergites with a pair of smooth, diverging grooves (fig. 21); ovipositor normal (fig. 19), with small dorsal nodus and ventral teeth.

**Distribution.** — South Palaearctic: one species. The biology is unknown.

**Victoroviella deserticola** Tobias  
(figs. 13—21)

Tobias, 1975: 962—964, figs. 1—3.

**Paratype**, ♀, length of body 6.6 mm, of fore wing 5.0 mm.

**Head.** — Antennal segments 34 (according to the original description 34—35), length of 3rd segment 1.6 times 4th segment, length of 3rd and 4th segment 2.1 and 1.3 times their width, respectively; length of penultimate segment 0.7 times its width (fig. 14); length of maxillary palp 0.6 times height of head; length of eye in dorsal view 1.3 times temple; temple subparallel (fig. 16) and long setose; POL : Ø ocellus : OOL = 8 : 3 : 12; frons flat and smooth; face with very long setae (fig. 13), remotely punctulate and weakly convex; clypeus depressed ventrally, its margin not differentiated; length of malar space 1.3 times basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.6 times its height; pronotal sides smooth (except for some punctures dorsally; fig. 13), and with a rather deep medial groove; mesopleuron smooth; episternal scrobe small, deep and round (fig. 13); mesoscutum and propodeum smooth; propodeal spiracle medium-sized, round, submedially situated (fig. 13).

**Wings.** — r : 3-SR : SR1 = 3 : 11 : 16; 1-SR+M straight; cu-a subinterstitial (fig. 15); 2-SR : 3-SR : r-m = 16 : 22 : 15; m-cu far antefurcal and slightly converging to 1-M posteriorly (fig. 15).

**Legs.** — Hind coxa smooth; length of femur, tibia and basitarsus of hind leg 2.8, 7.1 and 5.2 times their width, respectively; length of hind tibial spurs 0.4 and 0.5 times hind basitarsus; hind tibia with much longer setosity dorsally than ventrally; fore tibia with a row of five short spines.

**Metasoma.** — Length of 1st tergite 1.1 times

its apical width, its surface smooth (fig. 21); glymma completely absent; 2nd and 3rd tergites smooth; 2nd tergite with a pair of short, smooth and converging grooves medio-anteriorly (fig. 21); rest of metasoma smooth and rather depressed; length of ovipositor sheath 1.19 times fore wing; hypopygium large and acutely protruding medio-apically (fig. 13).

**Colour.** — Brownish-yellow; apex of mandibles, apex of antenna, wing veins partly, and pterostigma medio-anteriorly, dark brown; ovipositor sheath black; pronotum dorsally, anterior subalar protuberance, middle of mesopleuron, mesonotum medially, scapus and pedicellus anteriorly, and face, largely whitish; wing membrane hyaline.

**Paratype** in the Zoological Institute, Leningrad: "22/V. (19) 65, ksf. Kirpili, na strarinkus, T. Tokgaev", "Paratypus *Victoroviella deserticola* Tobias". Holotype in the Zoological Museum at Moscow from Turkmenia (Repetek), not examined.

**Note.** Not closely related to the other genera treated in this paper because of the peculiar shaped antenna, the longitudinal thin lamella of face, the shape of the scapus and the short marginal cell of fore wing.

**Lasiophorus** Haliday, 1833

Haliday, 1833: 213; Fahringer, 1930: 19 (key); Shenefelt, 1978: 1691—1694.

**Type-species:** *Bracon lanceolator* Fabricius, 1804 (monotypy).

**Diagnosis.** — Scapus very slender (fig. 23), widened apically and ventrally distinctly longer than dorsally (fig. 32); antennal sockets (toruli) protruding (figs. 23, 26); apex of antenna with short, not distinctly differentiated spine (fig. 35); face medially (just above clypeus) with a large, thick and rugose horn (figs. 23, 26, 27), or with spoon-shaped or tuberculiform protuberance; clypeus with no ventral carina; notauli absent; mesoscutum completely setose; scutellar sulcus narrow and finely crenulate (fig. 28); metanotum with no medial carina; vein 1-R1 of fore wing much longer than pterostigma (fig. 31; as in the other genera); vein m-cu of fore wing shortly antefurcal, converging to vein 1-M posteriorly (fig. 31); vein 1-SR+M of fore wing straight, but basally weakly curved; vein r-m of hind wing long and straight (fig. 31); marginal cell of hind wing subparallel-sided apically (fig. 31); hind tibial spurs with indistinct

and very short setosity, almost completely glabrous (fig. 29); tarsal claws setose and with no lobe (fig. 33); hind tarsus with ventral row of setae; dorso-lateral carinae of 1st tergite distinct and complete; dorsal carinae of 1st tergite absent (fig. 34); 2nd tergite anteriorly depressed and with a medial ridge instead of mediobasal area (fig. 34); antero-lateral grooves of 3rd and 4th tergites smooth and shallow, not reaching lateral margin of tergite (fig. 23); 2nd suture of metasoma distinct and smooth (fig. 34); no segments (except 1st) with sharp lateral crease; ovipositor normal (fig. 22), with small dorsal nodus and small ventral teeth.

**Distribution.** — Neotropical: four species. The biology is unknown.

### Lasiophorus lanceolator (Fabricius) (figs. 22—34)

*Bracon lanceolator* Fabricius, 1804: 106.

*Lasiophorus lanceolator*; Shenefelt, 1978: 1692; Van Achterberg, 1982: 137 (lectotype designation).

*Bracon nigriceps* Brullé, 1846, 334—335. **Syn. nov.**

*Lasiophorus nigriceps*; Shenefelt, 1978: 1692—1693.

**Lectotype**, ♀, length of body 16.2 mm, length of fore wing 14.5 mm.

**Head.** — Antennal segments 73, length of 3rd 1.7 times 4th segment, length of 3rd and 4th segments 2.2 and 1.3 times their width, respectively; penultimate segment of antenna 1.2 times as long as wide; length of maxillary palp 0.9 times height of head; temples weakly narrowed posteriorly (fig. 27); POL : Ø of ocellus : OOL = 4 : 5 : 10; frons laterally flat, but medially narrowly depressed (fig. 27); face apart from the horn, rather concave, coriaceous, rather mat (fig. 26); length of malar space 0.9 times basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.7 times its height; pronotal sides smooth, except for some punctulation (fig. 23); meso- and metapleuron punctulate; episternal scrobe absent, except for an indistinct remnant; scutellar sulcus narrow and shallowly crenulate (fig. 28); mesoscutum and scutellum sparsely punctulate (fig. 28); surface of propodeum punctulate; propodeal spiracle elliptical, rather large and situated behind middle of propodeum (fig. 23).

**Wings.** — Fore wing: angle between 1-SR and C+SC+R about 35° (fig. 31); r : 3-SR : SR1 = 8 : 43 : 58; cu-a postfurcal, long; 1-CU1 : 2-CU1 = 1 : 20; 2-SR : 3-SR : r-m = 19 : 43 : 17; r-m sinuate (fig. 31).

**Legs.** — Hind coxa punctulate; length of fe-

mur, tibia, and basitarsus of hind leg 4.6, 12.9, and 8.6 times their width, respectively; length of hind tibial spurs 0.35 and 0.5 times hind basitarsus; fore tibia with many spines (fig. 30).

**Metasoma.** — Length of 1st tergite 1.7 times its apical width, its surface mainly smooth, punctulate medially and sublateral grooves crenulate anteriorly (fig. 34); glymma present, shallow (fig. 23); metasoma smooth behind the 1st tergite, rather compressed; length of ovipositor sheath 2.08 times fore wing; hypopygium very large and truncate apically (fig. 23).

**Colour.** — Yellowish-brown; head, antenna, propleura, coxae partly, hind leg (except trochanters partly, base and apex of femur, and basal half of tibia), 5th—7th tergites and ovipositor sheath dark brown or blackish; palpi partly infuscated; wing membrane yellowish, but fore wing basally (shortly), apically and a band near pterostigma, dark brown (fig. 31); pterostigma and basal half of pterostigma, dark brown, but rest of pterostigma (light) brown.

**Lectotype** in the Copenhagen Museum: "Type", "Essequibo, Smidt, Mus: de Sehestedt, *Bracon lanceolator* Fabr." (Essequibo is a river in Guyana). Paralectotypes: 2 ♀, very similar to lectotype. In the Rijksmuseum van Natuurlijke Historie at Leiden are 11 ♀ and 1 ♂. The male from Surinam (Avanavero, 25.viii.1973, D. C. Geijskes) has the facial horn about half the size of the ♀ and undivided apically, body more densely setose, and base of fore wing yellowish. The females originate from Trinidad (Tacariqua, 500—600 m, 10.ix.1953, G. F. Mees) and Surinam (Republiek, 23.xi.1963, D. C. Geijskes and 31.iii.1963, P. H. van Doesburg; Kabalebo River, near Avanavero Falls, 14.ix.1965, and Brownsberg, 450—480 m, 16.xii.1973, both G. F. Mees; Mapane area, camp 8, 27 & 28.v.1963, and Zanderij, 21—25.vii.1963, both J. van der Vecht; Matta, 1.viii.1945; Wilhelminageberge, 16.viii.1943; and Moengotapoe, 24.ix.1948, all D. C. Geijskes).

**Variation.** — Length of fore wing 13.8—17.8 mm, of body 15.8—19.5 mm; length of ovipositor sheath 1.84—2.09 times fore wing; antennal segments 73—81. The known distribution is from Panama to Peru and Brazil.

**Note.** The statement of Fabricius (1804: 106): "Aculeus excertus niger, longitudine corporis" leads to the misinterpretation of *lanceolator* by Fahringer. Actually the ovipositor is somewhat less than twice length of the body. A syntype of *Bracon nigriceps* Brullé, 1846, in the Paris Mu-

seum has been examined. Another specimen may be present in the Spinola Collection (Turin) via Audinet-Serville.

**KEY TO SPECIES OF THE GENUS *Lasiophorus***  
HALIDAY

(after Fahringer, 1930, modified)

1. Length of ovipositor sheath about twice length of fore wing; wings banded ..... 2
- Length of ovipositor sheath less than length of fore wing, about as long as metasoma; wings not clearly banded ..... 3
2. Middle of 1st—4th tergites black; (Guyana); (dark form of *lanceolator*?) .....  
..... *fortispinus* Cameron
- Middle of 1st—4th tergites yellowish; (Panama to Peru and Brazil) .....  
..... *lanceolator* (Fabricius)
3. Pterostigma dark brown or blackish; facial protuberance spoon-shaped, concave medially and truncate apically, regular; apex of metasoma blackish; (Ecuador) .....  
..... *semirufus* Fahringer
- Pterostigma yellowish with its base and apex blackish; facial protuberance irregular tuberculiform; apex of metasoma yellowish; (Joinville Isl.) ..... *polaris* Fahringer

**Malagopsis** gen. nov.

Type-species: *Plaxopsis grandidieri* Szépligeti, 1913.

**Etymology:** from the combination of "Malagasy" and "Plaxopsis" because this genus is close to *Plaxopsis* and is only known from Malagasy. Gender: masculine.

**Diagnosis.** — Scapus medium-sized, ventrally strongly protruding (fig. 37) and inner aspect of its apex not emarginate (fig. 38); apex of antenna with short spine (fig. 41); face with a pair of large protuberances in front of antennal sockets (fig. 44); face very deeply concave medially, ventrally bordered by a sublamelliform semicircular protuberance (absent in ♂ and exceptionally in small ♀). Protuberance medially with a carina connected to a medial carina of the face (figs. 47, 49, 50); clypeus with a ventral carina; notauli shallowly impressed anteriorly (fig. 45); scutellar sulcus narrow and shallow; scutellum with no pit; metanotum with no medial carina; vein cu-a of fore wing slightly postfurcal; vein 1-M of fore wing somewhat bent posteriorly (fig. 42); vein m-cu of fore wing shortly antefurcal, slightly converging to vein 1-M posteriorly (fig. 39); vein 1-SR+M of fore wing bent basally; vein 1r-m of hind wing distinctly

curved (fig. 39); marginal cell of hind wing parallel-sided subapically; tarsal claws basally pectinate and with no lobe (fig. 46); hind tarsus with ventral row of setae; hind spurs setose; dorso-lateral carinae of 1st tergite lamelliform and complete (fig. 35); dorsal carinae of 1st tergite complete in posterior two-thirds of tergite, lamelliform and enclosing a long subpentagonal elevated area (fig. 48); 2nd tergite with smooth subtriangular medio-basal area, surrounded by sparsely crenulate grooves and with wide, posteriorly diverging antero-lateral grooves (fig. 48); 2nd suture obsolete laterally, rather deep and strongly crenulate medially (fig. 48); 3rd tergite with incomplete antero-lateral grooves; 2nd and 3rd tergites with sharp lateral crease; 4th and 5th tergites strongly convex (fig. 35); ovipositor with normal apex, with small nodus and teeth.

**Distribution.** — Afrotropical (Madagascar): one species. Parasites of Anthribidae (Coleoptera).

**Malagopsis grandidieri**

(Szépligeti) comb. nov.

(figs. 35—50)

*Plaxopsis grandidieri* Szépligeti, 1913: 419.

*Lasiophorus grandidieri*; Shenefelt, 1978: 1691.

*Lasiophorus seyrigi* Granger, 1949: 34—36, fig. 32;

Shenefelt, 1978: 1694. **Syn. nov.**

Holotype, ♀, length of body 11.9 mm, of fore wing 10.5 mm.

**Head.** — Antennal segments 64, length of 3rd segment 1.4 times 4th segment, length of 3rd and 4th segments 1.7 and 1.2 times their width, respectively; penultimate segment of antenna 1.3 times its width; length of maxillary palp 0.8 times height of head; groove between eye and antennal socket wide and rather deep (figs. 35, 47); eye slightly emarginate (fig. 47); length of eye in dorsal view 1.4 times temple; temples somewhat narrowed posteriorly (fig. 44); POL : Ø ocellus : OOL = 4 : 3 : 8; frons weakly concave, with shallow medial groove (fig. 44); face convex laterally, coriaceous and depressed beside clypeus (fig. 47); length of malar space equal to basal width of mandible; malar suture distinct and narrow (fig. 35).

**Mesosoma.** — Length of mesosoma 1.4 times its height; pronotal sides and mesopleuron smooth; episternal scrobe small, droplet-shaped (fig. 35); metapleuron punctulate; mesoscutum smooth and largely glabrous; surface of propodeum punctulate laterally, rest smooth; propodeal spiracle rather large, wide elliptical and sit-

uated just behind middle of propodeum.

**Wings.** — Fore wing: angle between veins 1-SR and C+SC+R of fore wing  $58^\circ$  (fig. 42); r : 3-SR : SR1 = 5 : 23 : 35; 1-CU1 : 2-CU1 = 1 : 38; 2-SR : 3-SR : r-m = 10 : 23 : 10.

**Legs.** — Hind coxa smooth; length of femur, tibia and basitarsus of hind leg 2.9, 7.8 and 4.0 times their width, respectively; length of hind spurs 0.20 and 0.25 times hind basitarsus.

**Metasoma.** — Length of 1st tergite 0.9 times its apical width, its surface largely smooth, medially with some wide punctures and weakly concave, and laterally with some coarse crenulae (fig. 48); glymma shallow and crenulate (fig. 35); metasoma behind 2nd tergite medially smooth, and 3rd—6th tergites punctate latero-posteriorly (fig. 35); length of ovipositor sheath 0.59 times fore wing; hypopygium large, and acute apically (fig. 35).

**Colour.** — Yellowish-brown; head (except black middle of facial depression and of lamella, stemmaticum, and area behind it), and pronotal sides dorso-posteriorly, ivory; wing membrane brownish; pterostigma and veins rather dark brown.

Holotype in Zoologisches Museum Berlin: "S. W. Madagascar, Tulear, Voeltzkow, S., 1.1904", "*Bracon grandidieri* Sauss., det. Dr. Enderlein" (incorrect!), "Type", "*Plaxopsis grandidieri* n. sp." (in Szépligeti's handwriting). Syntype-series of *Malagopsis seyrigi* (Granger, 1949) consists of 15 ♀ and 1 ♂. The ♀ from Diego ("Madagascar, Diego, xi.29, A. Seyrig") in the Muséum National d'Histoire Naturelle at Paris is here designated as lectotype. Judging from this series of *grandidieri* there is considerable allometric variation in the size of the facial lamella and flanges, and the punctuation of the 5th and 6th tergites. The dark patch on the pronotum may be distinct but (especially larger) specimens have this patch absent or obsolescent.

**Variation.** — Length of fore wing 7.9—10.5 mm (♂: 7.9 mm); length of body 8.8—11.9 mm (♂: 8.8 mm); length of ovipositor sheath 0.59—0.73 times fore wing; antennal segments 57—66 (♂: 55); facial depression deep or moderately depressed (always distinct in ♀, shallow in ♂); facial protuberances large to nearly absent (absent in ♂); 3rd sternite completely yellowish or with blackish patch, sometimes also 2nd and 4th sternites with such patch.

#### Deltaphyma gen. nov.

Type-species: *Deltaphyma horstoki* sp. nov.

**Etymology:** from "delta" (Greek capital letter, shaped like a triangle) and "phyma" (Greek for "growth") because of the peculiar triangular protuberance of the face. Gender: neuter.

**Diagnosis.** — Scapus robust, ventrally much longer than dorsally, surpassing pedicellus (fig. 54) and inner aspect of scapus distinctly emarginate (fig. 56); face convex, with spoon-shaped lamella, with above it a triangular lamella, with its corners (especially the top corner) longer than its sides (figs. 58, 60); clypeus without carinae; with deep groove from eye to antennal socket (fig. 52); notaui complete, shallow (fig. 63); scutellar sulcus very shallow and narrow, nearly smooth (fig. 63); scutellum with no pit; metanotum without carina; vein cu-a of fore wing subinterstitial; vein 1-M of fore wing straight (fig. 55); vein m-cu of fore wing shortly antefurcal, slightly converging to vein 1-M posteriorly; vein 1-SR+M of fore wing evenly curved (fig. 59); vein 1r-m of hind wing straight (fig. 55); marginal cell of hind wing parallel-sided apically; tarsal claws yellowish pectinate basally, without lobe (fig. 66); hind femur densely setose dorsally, ventrally sparsely, without distinct flange apically (fig. 64); hind tarsus without distinct ventral row of setae; hind spurs setose; dorso-lateral carinae of 1st tergite complete and lamelliform behind the spiracle, absent in front of spiracle (figs. 52, 65); dorsal carinae of 1st tergite completely absent (fig. 65); 2nd tergite with droplet-shaped, coriaceous medio-basal area, ending posteriorly in distinct keel, without distinct antero-lateral area (fig. 65); 2nd tergite projecting over 2nd suture (fig. 52); 2nd suture rather shallow and only medially crenulate (fig. 65); 3rd and 4th tergites with sharp lateral crease; 4th and 5th tergites rather flat (fig. 52); ovipositor normal, with small nodus and teeth (fig. 57).

**Distribution.** — Afrotropical: one species. The biology is unknown.

#### Deltaphyma horstoki sp. nov.

(figs. 51—66)

Holotype, ♀, length of body 18 mm, of fore wing 14.5 mm.

**Head.** — Antennal segments incomplete, 51, length of 3rd segment 1.7 times 4th segment, length of 3rd and 4th segments 2.2 and 1.3 times their width, respectively; length of maxillary palp equal to height of head; eyes slightly emarginate (fig. 61); length of eye in dorsal view 1.1 times temple; temple subparallel-sided behind eyes (fig. 62); POL : Ø ocellus : OOL =

3 : 5 : 15; frons smooth, distinctly concave behind antennal sockets, medially with low evaluation (fig. 62); face finely transversely striate, with some coarse striae; malar suture distinct; length of malar space 0.8 times basal width of mandible.

Mesosoma. — Length of mesosoma 1.8 times its height; side of pronotum and mesopleuron smooth; episternal scrobe small and pit-shaped (fig. 52); metapleuron smooth; mesoscutal lobes largely glabrous and smooth; surface of propodeum punctulate laterally, rest smooth; propodeal spiracle medium-sized, rather elliptical and just behind middle of propodeum.

Wings. — Fore wing: angle between 1-SR and C+SC+R 55° (fig. 59); r : 3-SR : SR1 = 6 : 22 : 27; 2-SR : 3-SR : r-m = 9 : 22 : 10.

Legs. — Hind coxa smooth; length of femur, tibia and basitarsus of hind leg 3.9, 9.9 and 6.6 times its width, respectively; length of spurs of hind tibia 0.3 and 0.4 times hind basitarsus.

Metasoma. — Length of 1st tergite 1.2 times its apical width, its surface coriaceous at medial elevation, rest smooth; medial area of 2nd tergite surrounded by some rugae, rest smooth (fig. 65); 3rd and 4th tergites distinctly striate mediobasally, rest of metasoma smooth (fig. 52); length of ovipositor sheath 0.6 times fore wing; hypopygium large and acute apically.

Colour. — Brownish-yellow; antenna, stemmaticum largely, metasoma behind 1st tergite (but medio-basal area of 2nd tergite yellowish), ovipositor sheath, middle telotarsus, hind tibia, spurs, and hind tarsus, blackish; basal third of wings, pterostigma (except its darkbrown apex), patch below pterostigma and near vein r-m of fore wing, more or less yellowish; rest of wings dark brown.

Holotype in the Rijksmuseum van Natuurlijke Historie at Leiden: "Horstok, Pr. b. Sp. (= Cape Town)", "Museum Leiden, *Bracon servilei* Brullé" (incorrect!).

Note. This species is named after its collector, Dr. H. B. van Horstok, a physician who collected for the Leiden Museum in South Africa during the period 1825—1835 († ca. 1838).

#### *Zanzopsis* gen. nov.

Type-species: *Plaxopsis liogaster* Szépligeti, 1913.

Etymology: from a combination of "Zanzibar" and "Plaxopsis", because the type species originates from Zanzibar and is closely related to the genus *Plaxopsis*. Gender: masculine.

Diagnosis. — Scapus rather slender (fig. 67), ventrally slightly longer than dorsally (fig. 69) and its inner aspect not emarginate apically; apex of antenna without spine, acute and setose (fig. 81); face with large medial protuberance, surmounted by a W-shaped carina and next to protuberance somewhat depressed (figs. 75, 77); dorsal carina of clypeus nearly complete (fig. 75); clypeus ventrally cariniform (fig. 77); groove from eye to antennal sockets shallow and narrow (fig. 67); notaular anteriorly shallowly impressed, rest absent (fig. 76); scutellar sulcus narrow and distinctly crenulate (fig. 76); scutellum with minute pit medio-anteriorly; metanotum with very short medial carina (fig. 76); vein cu-a of fore wing postfurcal (fig. 70); vein 1-M of fore wing straight; vein m-cu of fore wing antefurcal, slightly converging to vein 1-M posteriorly (fig. 70); vein 1-SR+M of fore wing distinctly bent subbasally (fig. 71); vein 1r-m of hind wing straight; marginal cell of hind wing strongly narrowed apically (fig. 70); tarsal claws basally pectinate, without lobe (fig. 78); hind femur dorsally densely and ventrally sparsely setose, without apical flange (fig. 79); hind tarsus without ventral row of setae; hind spurs sparsely setose; dorso-lateral carinae of 1st tergite distinct behind spiracles, lamelliform, in front of spiracles absent (figs. 67, 82); dorsal carinae of 1st tergite absent, except for a weak basal elevation (fig. 82); 2nd tergite not projecting above 2nd suture (fig. 67), without antero-lateral grooves (only depressed sublaterally), and with smooth medio-basal triangular area surrounded by a crenulate depression (fig. 82); 2nd suture deep, completely and coarsely crenulate (fig. 82); 3rd and 4th tergites with crenulate antero-lateral grooves (fig. 67); 2nd and 3rd tergites with sharp lateral crease; 4th and 5th tergites rather flat (fig. 67); ovipositor normal, with minute nodus and distinct teeth (fig. 73).

Distribution. — Afrotropical and South Palaearctic (N. Africa): contains at least the following five species of which the type has been examined: *Zanzopsis liogaster* (Szépligeti, 1913), *Z. levis* (Szépligeti, 1914), *Z. pulchripennis* (Szépligeti, 1911), *Z. buettneri* (Szépligeti, 1914), and *Z. maculiceps* (Szépligeti, 1914). The biology is unknown.

#### *Zanzopsis liogaster* (Szépligeti) comb. nov. (figs. 67—82)

*Plaxopsis liogaster* Szépligeti, 1913: 419.

*Lasiophorus liogaster*; Shenefelt, 1978: 1692.

Holotype, ♀, length of body 15.3 mm, of fore wing 14.7 mm.

**Head.** — Antennal segments 74, length of 3rd segment 1.5 times 4th segment, length of 3rd and 4th segments 1.5 and 1.0 times their width, respectively, penultimate segment 1.2 times its width (fig. 81); length of eye in dorsal view 1.3 times temple; temple parallel-sided (fig. 74); POL : Ø ocellus : OOL = 4 : 5 : 14; frons flat, but shallowly concave near medial groove; face coriaceous and with some carinae (fig. 80); malar suture narrow; length of malar space 1.3 times basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.7 times its height; side of pronotum smooth and with medial groove; mesopleuron smooth, except for some punctulation ventrally; episternal scrobe shallow and narrow (fig. 67); metapleuron punctulate; mesoscutal lobes only setose near notauli, smooth, and convex; surface of propodeum punctulate, but smooth medially; propodeal spiracle nearly round, rather large and just behind middle of propodeum.

**Wings.** — Fore wing: angle between 1-SR and C+SC+R of fore wing 58° (fig. 71); r : 3-SR : SR1 = 6 : 25 : 22; 1-CU1 : 2-CU1 = 2 : 27; 2-SR : 3-SR : r-m = 10 : 25 : 13.

**Legs.** — Hind coxa smooth; length of femur, tibia and hind basitarsus of hind leg 3.4, 9.8, and 4.9 times their width, respectively; length of hind tibial spurs 0.3 and 0.4 times hind basitarsus.

**Metasoma.** — Length of 1st tergite 1.1 times its apical width, surface smooth, medially with a small, shallow depression with short carina (fig. 82); glymma narrow anteriorly (fig. 67); 2nd tergite smooth, except near basal area; 4th tergite crenulate anteriorly, rest of metasoma smooth (fig. 67); length of ovipositor sheath 0.78 times fore wing; hypopygium large, apically acute (fig. 67).

**Colour.** — Brownish-yellow; antenna, hind tibia and tarsus, and ovipositor sheath, blackish; metasoma and fore telotarsus, brown; middle telotarsus dark brown; basal third of wings, basal half of pterostigma, patch below pterostigma, area near vein r-m and below vein 2-SR+M of fore wing, yellowish; rest of pterostigma and wing membrane, dark brown.

Holotype in Museum Berlin: "Sansibar, C.

W. Schmidt", "Type", "*Plaxopsis liogaster* n. sp." (in Szépligeti's handwriting).

### **Plaxopsis Szépligeti, 1905**

Szépligeti, 1905: 1; Fahringer, 1931: 336 (key); Shenefelt, 1978: 1691 (as synonym of *Lasiophorus*).

Type-species: *Plaxopsis sjoestedti* Szépligeti, 1905 (monotypic). Gender: masculine.

**Diagnosis.** — Scapus medium-sized (fig. 84), in dorsal view about twice its width, apically truncate, not protruding ventrally (fig. 92) and inner aspect of apex not emarginate; face with pair of submedial depressions and near protuberance (rather) depressed (fig. 87); between clypeus and face with a large, lamelliform, spoonshaped protuberance, which is concave ventrally (figs. 84, 87) and sometimes with horn situated on it; clypeus with ventral carina; no distinct groove between eye and antennal socket; notauli shallow, but absent apically (fig. 89); scutellar sulcus rather wide and coarsely crenulate (fig. 89); scutellum with pit medio-basally; metanotum with short carina medially; vein cu-a of fore wing slightly postfurcal (fig. 91); vein 1-M of fore wing straight; vein m-cu of fore wing shortly antefurcal, distinctly converging to vein 1-M posteriorly (fig. 91); vein 1-SR+M of fore wing distinctly bent basally (fig. 91); vein 1r-m of hind wing straight; marginal cell of hind wing (sub)parallel-sided apically or slightly narrowed, only medially distinctly narrowed (fig. 91); tarsal claws setose (fig. 85); hind femur without flange apically, dorsally distinctly and ventrally sparsely setose (fig. 90); hind tarsus with ventral row of setae; hind spurs normally setose; dorso-lateral carinae complete (fig. 84); dorsal carinae of 1st tergite absent (fig. 93); 2nd tergite with smooth, subtriangular area medio-anteriorly, with pair of sublongitudinal grooves laterally and with pair of small smooth triangular areas anteriorly (fig. 93); 2nd tergite not projecting above 2nd suture; 2nd suture deep and coarsely crenulate; 3rd tergite with pair of nearly complete, crenulate antero-lateral grooves (fig. 93); 4th and 5th tergites rather flat, with incomplete antero-lateral grooves (fig. 84); ovipositor normal, with subapical nodus and with small teeth ventrally.

**Distribution.** — Afrotropical and South Pal-

nearctic (N. Africa): moderately sized genus.  
The biology is unknown.

**Plaxopsis sjöestedti Szépligeti**  
(figs. 83—93)

*Plaxopsis Sjöstedti* Szépligeti, 1905: 1—3, fig. 1.  
*Lasiophorus sjöestedti*; Shenefelt, 1978: 1694.

Holotype, ♀, length of body 16.1 mm, of fore wing 16.2 mm.

Head. — Antennal segments 64 (apical segments missing), length of 3rd segment 1.5 times 4th segment, length of 3rd and 4th segments 1.6 and 1.1 times their width, respectively; length of maxillary palp equal to height of head; length of eye in dorsal view 1.5 times temple; POL : Ø ocellus : OOL = 3 : 3 : 11; frons weakly concave; face smooth; clypeus largely flat and smooth; malar suture shallow; length of malar space 0.9 times basal width of mandible.

Mesosoma. — Length of mesosoma 1.7 times its height; side of pronotum and mesopleuron smooth; mesoscutal lobes largely glabrous, smooth and rather convex; surface of propodeum smooth, posteriorly rather depressed (fig. 93); propodeal spiracle rather large, subelliptical and at middle of propodeum (fig. 84).

Wings. — Fore wing: angle between 1-SR and C+SC+R 56° (fig. 91); r : 3-SR : SR1 = 9 : 50 : 51; 1-CU1 : 2-CU1 = 1 : 12; 2-SR : 3-SR : r-m = 24 : 50 : 22.

Legs. — Hind coxa indistinctly punctulate; hind and fore claws missing; length of femur, tibia, and basitarsus of hind leg 4.3, 10.8, and 6.1 times their width, respectively; length of spurs of hind tibia 0.3 and 0.4 times hind basitarsus.

Metasoma. — Length of 1st tergite 1.7 times its apical width, smooth (fig. 93); glymma narrow (fig. 84); 2nd tergite (except basal area) striate (fig. 93); rest of metasoma smooth; length of ovipositor sheath 0.84 times fore wing; hypopygium large and apically acute (fig. 84).

Colour. — Dark reddish-brown; head, palpi, apex of antenna, prothorax, metasoma ventrally (but posteriorly brownish) and 9th tergite, yellowish; wing membrane dark brown, but fore wing with subapical yellowish, incomplete band and below pterostigma with a small light area (fig. 91).

Holotype in the Stockholm Museum: "Camerun", "Sjöstedt", "Plaxopsis Sjöstedti n.g. n. sp." (in Szépligeti's handwriting).

**Plesiobracon GROUP**

The *Plesiobracon* group contains three genera known to me, which have the 1st tergite of the metasoma movably joined to the 2nd tergite, with strong and complete dorso-lateral carinae, the mesoscutum rather evenly setose and at the same time the propodeum with a strong and complete medio-longitudinal carina, the scapus is (sub)truncate apically and ovoid (figs. 97, 113), the clypeus has no dorsal carina, the angle between veins 1-SR and C+SC+R of fore wing more than 60°, vein cu-a of fore wing slightly postfurcal (figs. 98, 114), the laterope is absent, and the 2nd tergite has a pair of sublateral, converging or short longitudinal grooves (figs. 109, 121). The biology is unknown.

**KEY TO GENERA OF THE *Plesiobracon* GROUP**

1. First tergite without dorsal carinae (fig. 137); posterior margin of hind wing (but sometimes hardly) concave subbasally and shorter setose than surrounding fringe (fig. 136); head strongly constricted behind eyes (fig. 132); vein cu-a of hind wing reclivous (fig. 136); (Indo-Australian) ..... *Plesiobracon* Cameron
- First tergite with strong, united dorsal carinae (figs. 109, 121); posterior margin of hind wing about straight subbasally and evenly setose (figs. 104, 114); head rounded posteriorly (fig. 107, 117); vein cu-a of hind wing (nearly) straight (figs. 98, 114); (Afrotropical) ..... 2
2. Medial length of 5th tergite ca. 0.8 times medial length of 4th tergite behind basal depression (fig. 95); vein 2-SR of fore wing straight (fig. 98); 5th tergite straight latero-apically (fig. 95); antescutal depression present (fig. 95); propleuron without posterior flange (fig. 95); 2nd tergite with small medio-basal area (fig. 109); mesoscutum punctulate (fig. 108); propodeal spiracle situated submedially at propodeum (fig. 95); 4th tergite more or less protruding medio-apically; 2nd submarginal cell of fore wing slender (fig. 98) ... *Carinibracon* gen. nov.
- Medial length of 5th tergite (behind basal depression) 1.3—1.5 times medial length of 4th tergite (fig. 110); veins 2-SR of fore wing (rather) sinuate (fig. 114); 5th tergite oblique latero-apically (fig. 110); antescutal depression absent (fig. 110); propleuron with small posterior flange (fig. 110); 2nd

tergite without medio-basal area (fig. 121); mesoscutum finely rugose (fig. 116); propodeal spiracle situated in front of middle of propodeum (fig. 110); 4th tergite straight medio-apically (fig. 122); 2nd submarginal cell of fore wing robust (fig. 114) . . . . .  
Kenema gen. nov.

### **Plesiobracon** Cameron, 1903

Cameron, 1903: 123; Shenefelt, 1978: 1717.

Type-species: *Plesiobracon carinatus* Cameron, 1903 (monotypic). Gender: masculine.

**Diagnosis.** — Head strongly constricted behind eyes (fig. 132); apex of antenna with spine (fig. 130); ventral margin of clypeus cariniform and protruding (fig. 125); propleuron without posterior flange (fig. 123); anterior half of notaulari distinct, smooth, rest absent (fig. 133); mesoscutum only laterally punctulate; scutellar sulcus deep, rather wide and distinctly crenulate (fig. 133); metanotum with some rugae medially (fig. 133); propodeal spiracle medium-sized, nearly round and behind middle of propodeum (fig. 123); vein 2-SR of fore wing straight; vein cu-a of hind wing reclivous (fig. 136); posterior margin of hind wing concave (but hardly in *vierecki*), more shortly setose than surrounding fringe (fig. 136); tarsal claws with large, rounded submedial lobe (fig. 129); hind femur slender, its length about 4 times the maximum width (fig. 134); hind tibia with subapical transverse row of spiny setae (fig. 134); no ventral row of setae at hind tarsus; 1st tergite without dorsal carinae (fig. 137); 2nd tergite with a narrow triangular area medio-basally (fig. 137); 2nd suture wide, straight and crenulate (fig. 137); 4th tergite protruding medio-posteriorly (fig. 137); 2nd—5th tergites with sharp lateral crease; medial length of 5th tergite about 0.6 times medial length (behind basal depression) of 4th tergite (fig. 123); 5th tergite nearly straight latero-apically (fig. 123); hypopygium large, acutely protruding beyond metasomal apex, medio-basally unsclerotized.

**Distribution.** — Indo-Australian: two species. The 2nd species (besides the type-species from Borneo) is *Iphiaulax vierecki* Strand, 1911 (= *braconiformis* Strand, 1911, nec Szépligeti, 1904) from New Guinea according to Dr. D. Quicke (in litt.).

### **Plesiobracon carinatus** Cameron, 1903 (figs. 123—137)

*Plesiobracon carinata* Cameron, 1903: 123; Shenefelt, 1978: 1717.

Lectotype, ♀, length of body 5 mm, of fore wing 5.8 mm.

**Head.** — Antennal segments 44, length of 3rd segment equal to 4th segment, length of 3rd and 4th segments both 1.9 times their width, penultimate segment 2.3 times its width (fig. 130); length of maxillary palp 0.8 times height of head; eye glabrous, not emarginate; length of eye in dorsal view 3.5 times temple; POL : Ø ocellus : OOL = 7 : 7 : 20; frons flat, except for a medial groove (fig. 132); face indistinctly punctulate and rather flat; clypeus flat and smooth; length of malar space equal to basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.4 times its height; side of pronotum smooth, except for a crenulate groove medially; mesopleuron largely punctulate; episternal scrobe distinct and isolated; scutellum smooth; anterior half of propodeum punctulate, posteriorly smooth, long whitish setose.

**Wings.** — Fore wing: angle between 1-SR and C+SC+R 81°; r : 3-SR : SR1 = 5 : 17 : 31; 1-CU1 : 2-CU1 = 1 : 13; 2-SR : 3-SR : r-m = 10 : 17 : 6.

**Legs.** — Hind coxa smooth; length of femur, tibia, and basitarsus of hind leg 4, 8.2, and 6.8 times their width; length of spurs of hind tibia 0.30 and 0.35 times hind basitarsus.

**Metasoma.** — Length of 1st tergite 0.9 times its apical width, reticulate-rugose postero-medially, laterally with wide crenulate groove; spiracles directed dorsally; 2nd—5th tergites finally longitudinally rugose, 3rd—5th tergites with smooth apical rim (figs. 123, 137); 3rd tergite without lateral grooves; metasoma behind 5th tergite smooth; length of ovipositor sheath 1.32 times fore wing.

**Colour.** — Blackish-brown; middle of frons, temples dorsally, and vertex, dark brown; rest of head, fore leg, and metasoma ventro-basally, yellowish-brown; pterostigma and parastigma, dark brown; middle femur, tibia and tarsus, brown; palpi light yellowish; wing membrane subhyaline.

Lectotype in British Museum (Natural History), London: "Type", "BM. Type Hym., 3.c.603", "*Plesiobracon carinata* Cam., Type, Borneo" (in Cameron's handwriting), "Kuching, Feb. 3, 1902", "Cameron Coll. 1903—121". Lectotype here designated. In the Kuch-

ing Museum I examined 2 ♀ in the collection under "carinata": one specimen collected April 1, 1902, the 2nd specimen at May 24, 1903. Because of the date of capture of the 2nd specimen, this specimen is excluded from the type-series. The other ♀ is considered to be a paralectotype. It differs from the lectotype by a narrow antescutal depression.

### *Carinibracon* gen. nov.

Type-species: *Carinibracon danielssoni* sp. nov.

**Etymology:** from "carina" (Latin for "keel") and "Bracon", because it is closely related to the genus *Bracon*, but it possesses several carinae (propodeum, 1st and 2nd tergites) which are normally absent in *Bracon*. Gender: masculine.

**Diagnosis.** — Head rounded posteriorly (fig. 107); apex of antenna without spine, setose (fig. 99); ventral carina of clypeus present, protruding (figs. 95, 103); propleuron without posterior flange (fig. 95); mesoscutum punctulate; notauli completely smooth (fig. 108); scutellar sulcus medium-sized, rather wide and crenulate (fig. 108); metanotum with short medial carina; propodeal spiracle round, near middle of propodeum (fig. 95); vein 2-SR of fore wing straight; 2nd submarginal cell of fore wing slender (fig. 98); vein cu-a of hind wing straight (fig. 104); posterior margin of hind wing nearly straight basally and evenly setose (fig. 104); tarsal claws with peculiar lamelliform lobe and with some pegs (fig. 100); hind femur robust, about 3.5 times its maximum width (fig. 102); hind tibia without subapical row of spiny setae (fig. 102); hind tarsus with distinct ventral row of setae; 1st tergite with dorsal carinae complete, meeting posteriorly, in front of strongly convex area (fig. 109); 2nd tergite with small subtriangular area medio-basally and with pair of weakly converging sublateral grooves (fig. 109); 2nd suture sinuate and crenulate (fig. 109); 4th tergite somewhat protruding medio-posteriorly; medial length of 5th tergite about 0.8 times medial length of 4th tergite behind basal depression (fig. 95); 5th tergite straight latero-apically (fig. 95); 2nd—6th tergites with sharp lateral crease; hypopygium large and acute apically (fig. 95).

**Distribution.** — Afrotropical: one species.

### *Carinibracon danielssoni* sp. nov. (figs. 94—109)

Holotype, ♀, length of body 4.7 mm, of fore wing 4.6 mm.

**Head.** — Antennal segments 35, length of 3rd segment 1.3 times 4th segment, length of 3rd and 4th segments 2.3 and 1.8 times their width, respectively, penultimate segment 1.7 times its width (fig. 99); length of maxillary palp 0.7 times height of head; eye glabrous and slightly emarginate (fig. 103); length of eye in dorsal view 1.8 times temple; POL : Ø ocellus : OOL = 3 : 3 : 7; frons nearly flat, coriaceous and with short groove near anterior ocellus (fig. 107); face largely coriaceous, but smooth above clypeus; length of malar space 0.8 times basal width of mandible.

**Mesosoma.** — Length of mesosoma 1.5 times its height; side of pronotum and mesopleuron smooth, but mesopleuron ventrally sparsely punctulate; episternal scrobe shallow (fig. 95); scutellum punctulate; surface of propodeum smooth and setose.

**Wings.** — Fore wing: angle between 1-SR and C+SC+R 70° (fig. 101); r : 3-SR : SR1 = 15 : 37 : 77; 1-CU1 : 2-CU1 = 2 : 25; 2-SR : 3-SR : r-m = 28 : 37 : 17.

**Legs.** — Hind coxa punctulate; length of femur, tibia and basitarsus of hind leg 3.5, 7.5 and 5 times their width, respectively; length of spurs of hind tibia 0.35 and 0.4 times hind basitarsus.

**Metasoma.** — Length of 1st tergite 0.8 times its apical width, largely smooth (fig. 109); 2nd tergite coarsely reticulate-rugose; 3rd—7th tergites finely rugulose, with narrow subapical transverse groove and posterior rim smooth (fig. 95); length of ovipositor sheath 0.8 times fore wing.

**Colour.** — Brownish-yellow; antenna (of scapus and pedicellus only outer side), pterostigma, veins, and ovipositor sheath, dark brown; wing membrane brownish.

**Holotype** in Entomological Museum, Lund: "Senegal, in forest, 1.5 km NE Djibélor, ca. 6.5 km SW Ziguinchor, 8.iii.1977. At light, 19.00—21.30. Loc. no. 23A, UTM 28PCJ575885", "Lund Univ., Syst. Dept. Sweden, Gambia/Senegal Febr.—March 1977, Cederholm, Danielsson, Larsson, Mireström, Norling, Samuelsson".

**Note.** — In existing keys the species runs to the genus *Cratocnema*, but *Cratocnema* differs e.g., by the presence of a dorsal carina at the clypeus. The descriptions of the *Cratocnema* spp. do not fit *C. danielssoni*.

It is a pleasure to me to dedicate this species to Mr. R. Danielsson (Lund), who has been very helpful in providing types and new taxa.

***Kenema* gen. nov.**

Type-species: *Kenema quickei* sp. nov.

Etymology: name based on the locality of the type. Gender: feminine.

Diagnosis. — Head rounded posteriorly (fig. 117); apex of antenna with small spine (fig. 111); ventral carina of clypeus not differentiated (fig. 120); propleuron with small posterior flange (fig. 110); mesoscutum finely rugose (fig. 116); notaui only anteriorly distinct and finely crenulate (fig. 116), rest absent; scutellar sulcus narrow and finely crenulate (fig. 116); metanotum with complete longitudinal carina; propodeal spiracle small, round and in front of middle of propodeum (fig. 110); vein 2-SR of fore wing sinuate (fig. 114); 2nd submarginal cell of fore wing robust (fig. 114); vein cu-a of hind wing straight; posterior margin of hind wing straight and evenly setose (fig. 114); tarsal claws with small acute lobe (fig. 118); hind femur moderately robust (fig. 119); hind tibia without row of spiny setae; hind tarsus with ventral row of setae; 1st tergite with dorsal carinae united medially, but medially rather weak (fig. 121); 2nd tergite without medial area and with short longitudinal grooves (fig. 121); 2nd suture distinctly sinuate and crenulate; 4th tergite straight medio-posteriorly (fig. 122); medial length of 5th tergite (behind basal, crenulate groove) 1.3—1.5 times medial length of 4th tergite (figs. 110, 122); 5th tergite oblique latero-apically (fig. 110); 2nd—5th tergites with sharp (cariniform) lateral crease.

Distribution. — Afrotropical: two species. The 2nd species will be described in a forthcoming paper.

***Kenema quickei* sp. nov.**

(figs. 110—122)

Holotype, ♂, length of body 6 mm, of fore wing 4.5 mm.

Head. — Antennal segments 52, length of 3rd segment 1.2 times 4th segment, length of 3rd and 4th segments 1.7 and 1.4 times their width, respectively, penultimate segment 1.4 times its width (fig. 111); length of maxillary palp 0.6 times height of head; length of eye in dorsal view 2.6 times temple; temple ruguloso-coriaceous; POL : Ø ocellus : OOL = 6 : 4 : 12; frons slightly convex, laterally rugose, medially coriaceous, and with shallow medial depression (fig. 117); stemmaticum comparatively strongly protruding (fig. 120); face transversely rugose; length of malar space equal to basal width of mandible.

Mesosoma. — Length of mesosoma 1.5 times its height; side of pronotum coriaceous, with some striae (fig. 110); mesopleuron coriaceous; episternal scrobe virtually absent; scutellum coriaceous; propodeum densely rugulose, medially-laterally shortly lamelliform and angularly protruding (fig. 110).

Wings. — Fore wing: angle between 1-SR and C+SC+R 61°; r-m distinctly sinuate and sclerotized (fig. 114); r : 3-SR : SR1 3 = 7 : 10 : 39; 2-SR : 3-SR : r-m = 11 : 10 : 11.

Legs. — Hind coxa coriaceous; length of femur, tibia, and basitarsus of hind leg 3.9, 8.2, and 5.2 times their width, respectively; length of spurs of hind tibia both 0.4 times hind basitarsus.

Metasoma. — Length of 1st tergite 0.4 times its apical width, basally smooth, behind dorsal carinae distinctly rugose; 2nd tergite rather coarsely reticulate; 3rd tergite reticulate-rugose; 4th and 5th tergites densely coriaceous-rugulose, with incomplete lateral grooves (fig. 110); 6th tergite shortly setose, exposed, smooth; 7th tergite glabrous; 2nd—5th tergites with acute lateral crease.

Colour. — Brownish-yellowish; antenna (except annulus) black; wing membrane slightly infuscated (but more pigmented near parastigma; fig. 115); anterior margin of fore wing (except base) blackish, rest of pterostigma and most veins, brown.

Holotype in Quicke Collection, Nottingham: "Kenema, Sierra Leone, Sept. 1981, D. Quicke". I am pleased to name this species after Dr. D. Quicke, who collected several interesting taxa in Africa.

Note. This new genus resembles the genus *Soter* Saussure, 1892 (= *Odontogaster* Szépligeti, 1906, *syn. nov.*), but *Soter* does not belong to the *Plesiobracon* group because it has the mesoscutum largely glabrous. Additionally it has the mesoscutum smooth, the 2nd submarginal cell is long, the 2nd tergite has converging grooves, the 5th tergite is serrate, and the spiracle of the propodeum is submedially situated.

## ACKNOWLEDGEMENTS

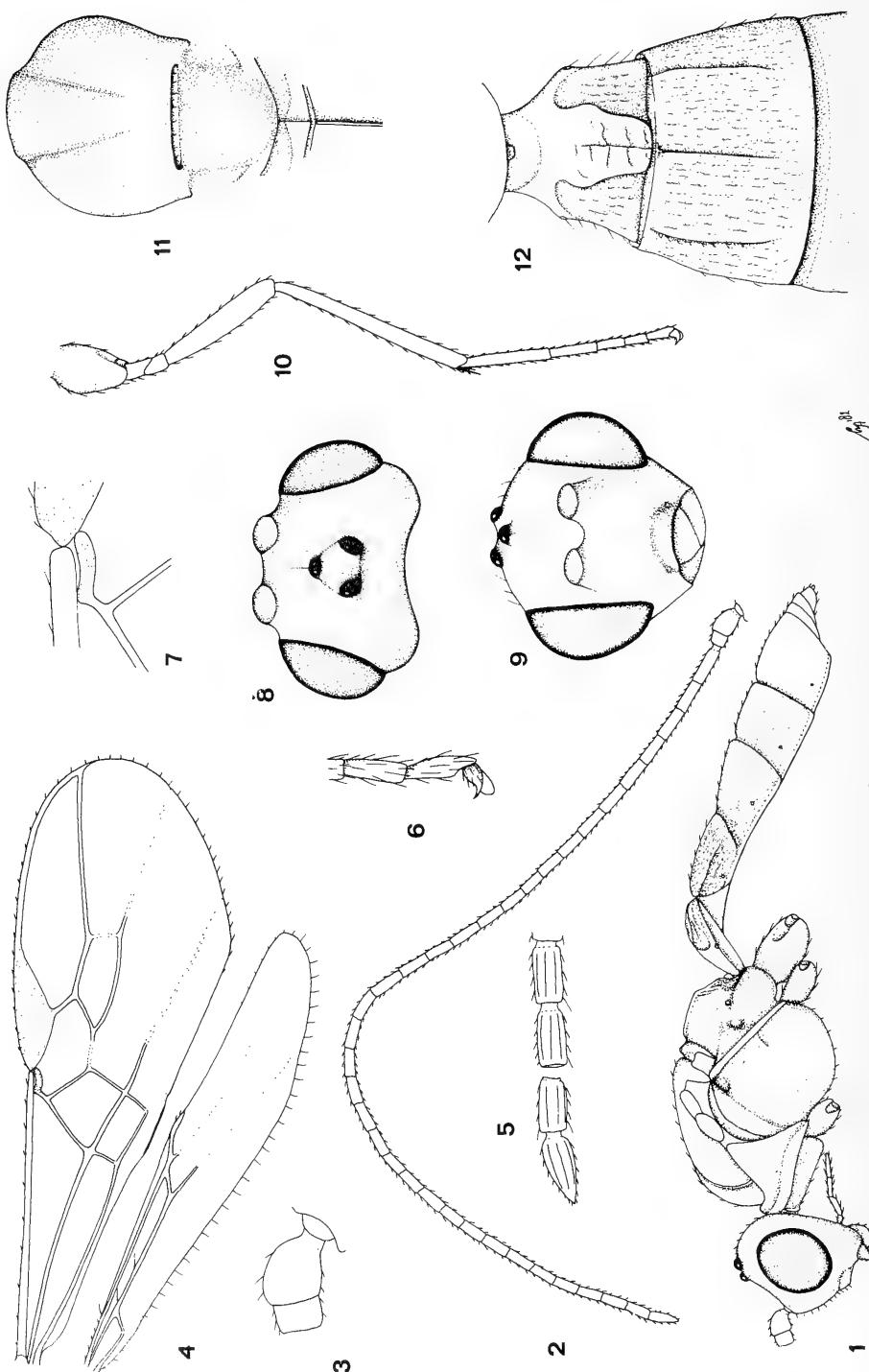
I wish to express my gratitude to the following persons for the loan of types and of new taxa, and for assistance during visits: Mr. R. Danielsson (Lund), Dr. J. Decelle (Tervuren), Mr. A. A. Hamid (Kuching), Dr. K.-J. Hedqvist (Stockholm), Mr. T. Huddleston (London), Mlle Dr. S. Kelner-Pillault (Paris), † Dr. E.

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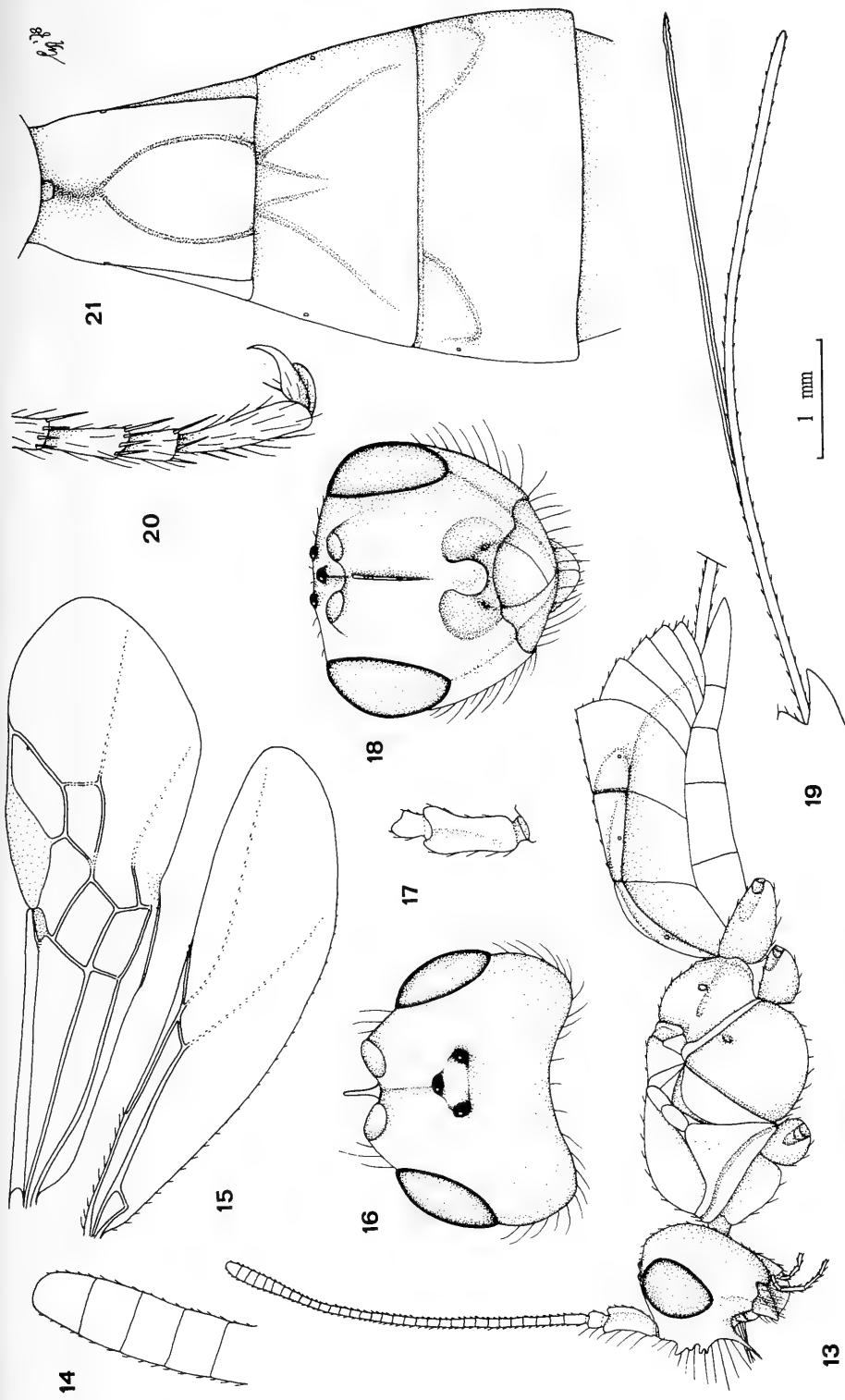
The Uyttenboogaart-Eliassen Stichting financially supported the visit to the Kuching Museum (Serawak).

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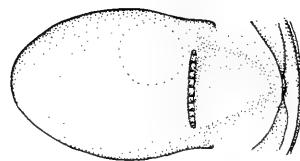
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Figs. 1-12. *Adeshoides aulicains* sp. nov., holotype, ♂. 1, habitus, lateral aspect; 2, antenna; 3, scapus and pedicellus, outer aspect; 4, wings; 5, apical segments of antenna; 6, hind claw; 7, detail of vein 1-SR of fore wing; 8, head, frontal aspect; 9, head, dorsal aspect; 10, hind leg, frontal aspect; 11, mesosoma, dorsal aspect; 12, hind leg, dorsal aspect. 1, 2, 4, 10: scale-line (= 1  $\times$ ); 3, 5-7: 2.5  $\times$ ; 8, 9, 11, 12: 1.6  $\times$ .

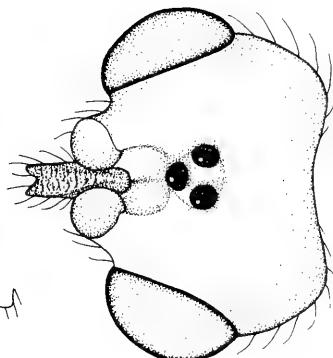


Figs. 13—21. *Victoroviella deserticola* Tobias, paratype, ♀. 13, habitus, lateral aspect; 14, apex of antenna; 15, wings; 16, head, dorsal aspect; 17, scapus and pedicellus, frontal aspect; 18, head, front aspect; 19, ovipositor; 20, fore claw; 21, 1st—3rd metasomal tergites. 13, 15, 19, scale-line (= 1 X); 16—18, 21: 2 X; 14, 20: 5 X.

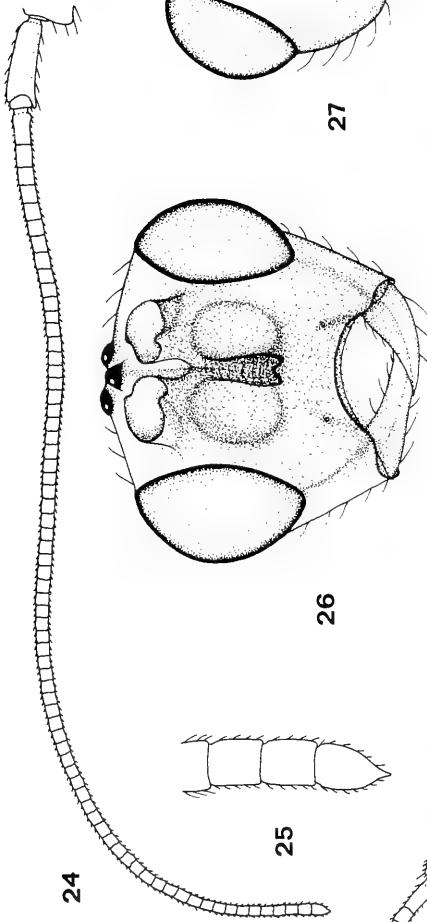


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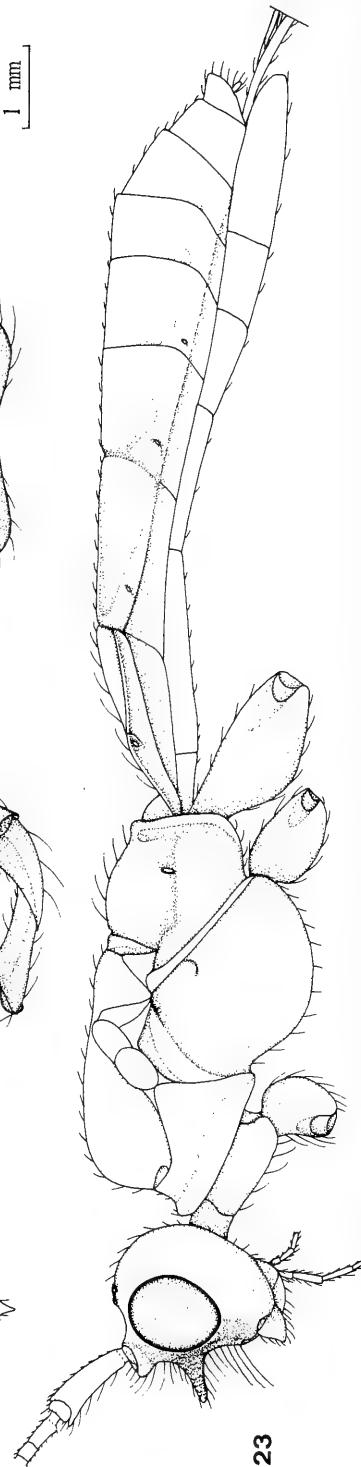


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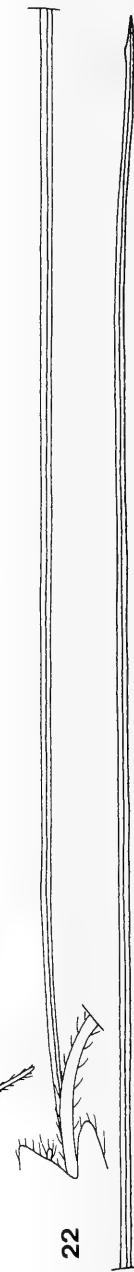
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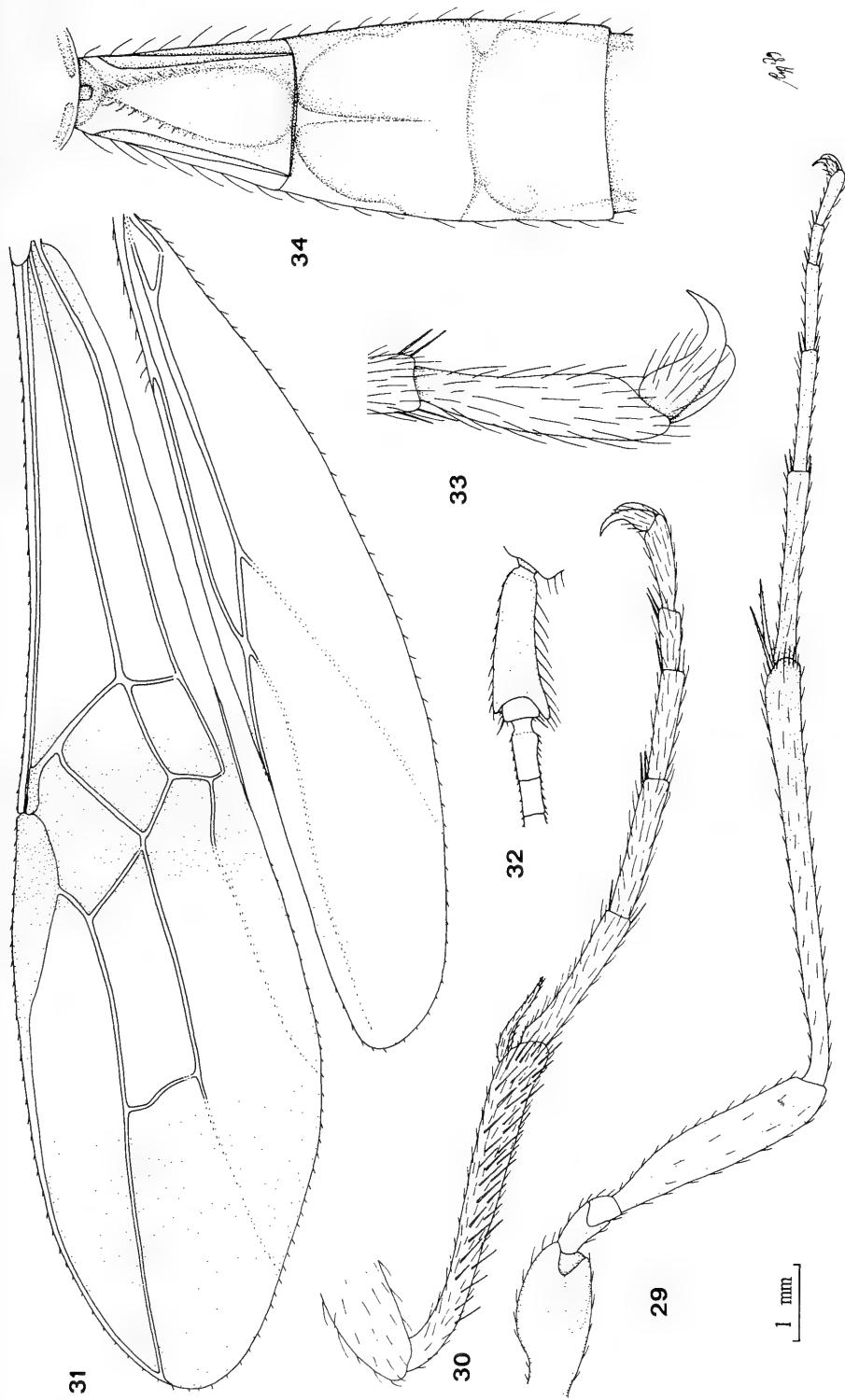


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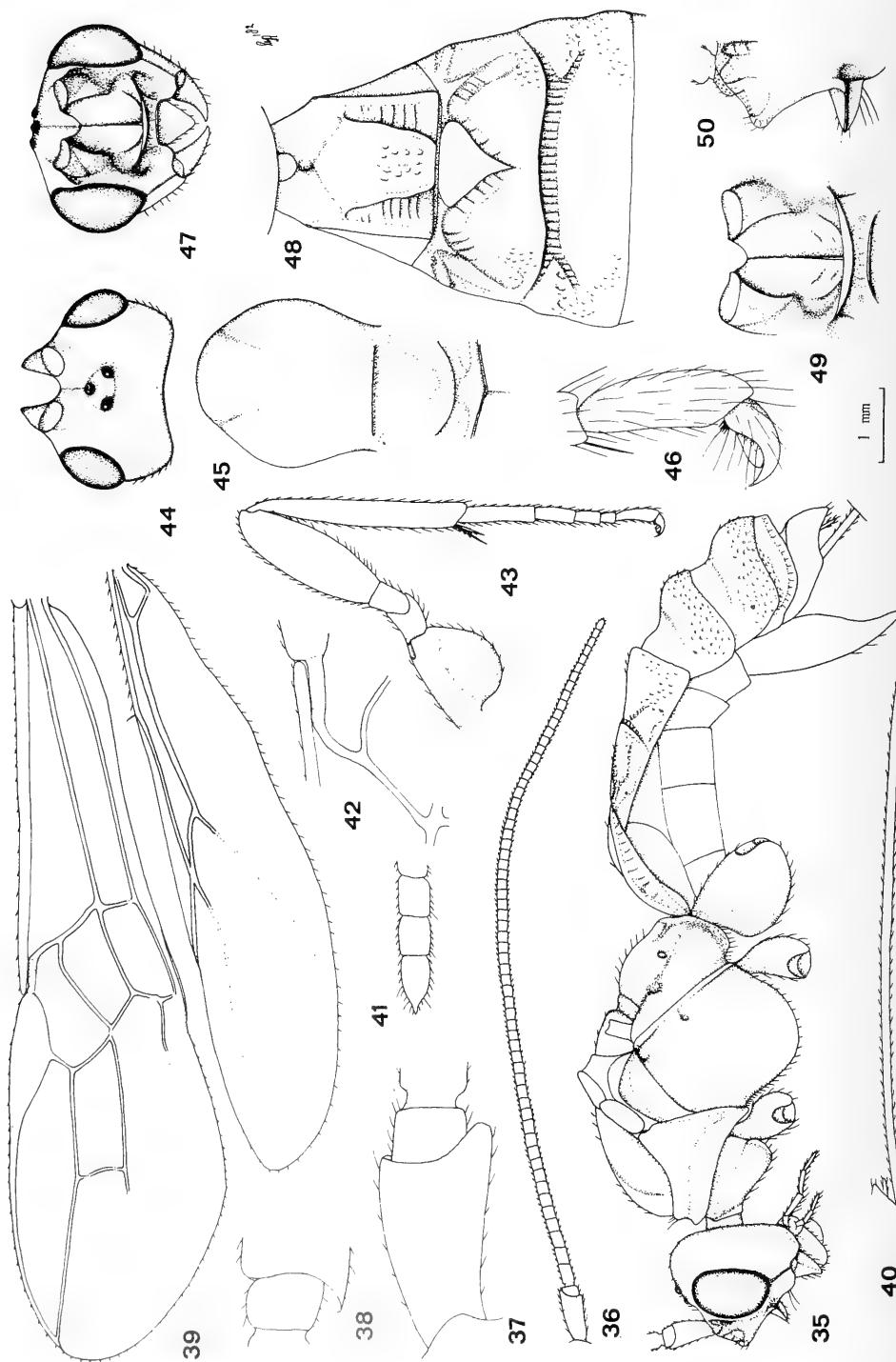
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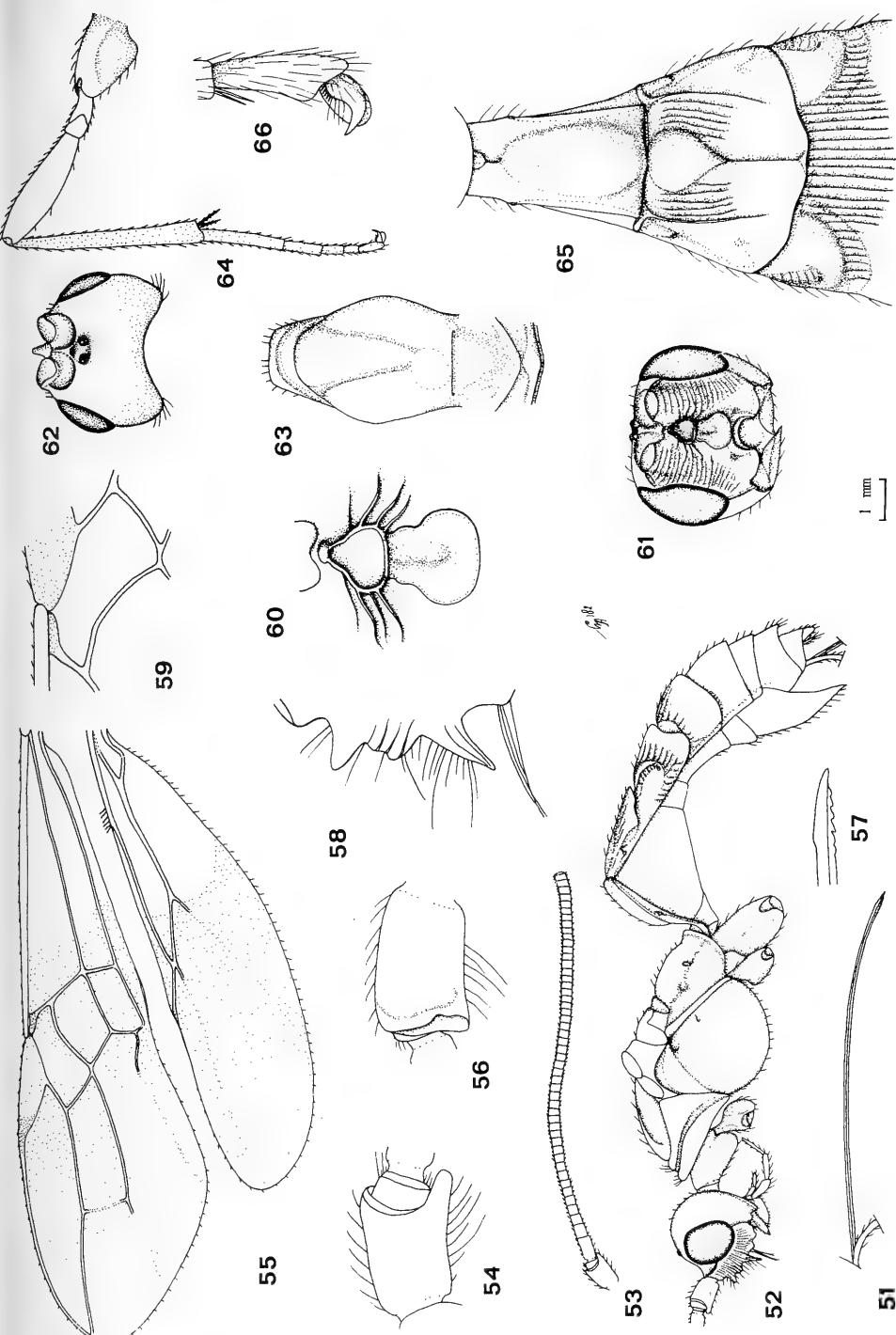
Figs. 22—28. *Lasiophorus lanceolator* (Fabricius), lectotype, ♀. 22, ovipositor; 23, habitus, lateral aspect; 24, antenna; 25, apex of antenna; 26, head, frontal aspect; 27, head, dorsal aspect; 28, thorax, dorsal aspect. 22—24; scale-line ( $= 1 \times$ ); 25, 5  $\times$ ; 26, 27, 28; 1.2  $\times$ .



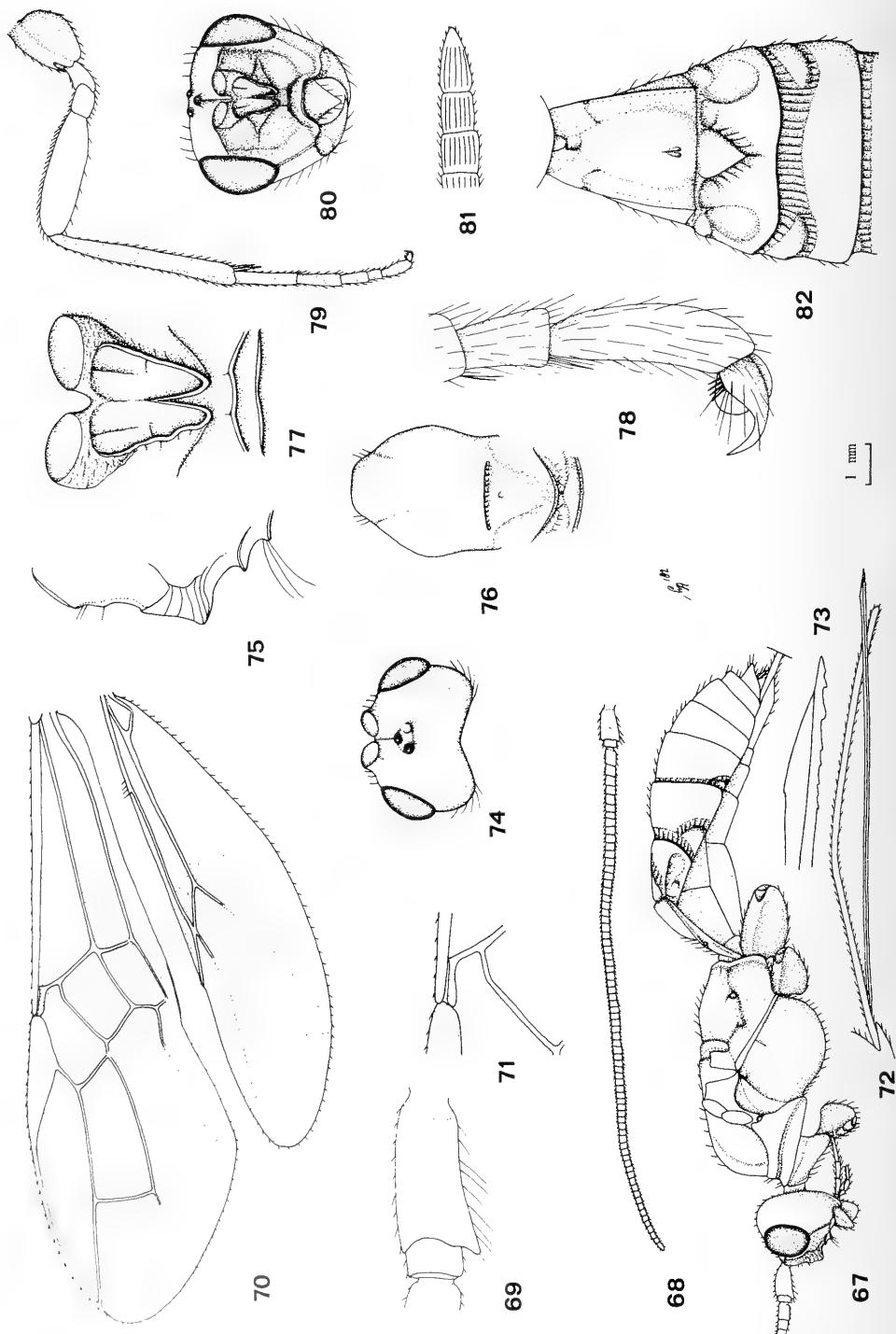
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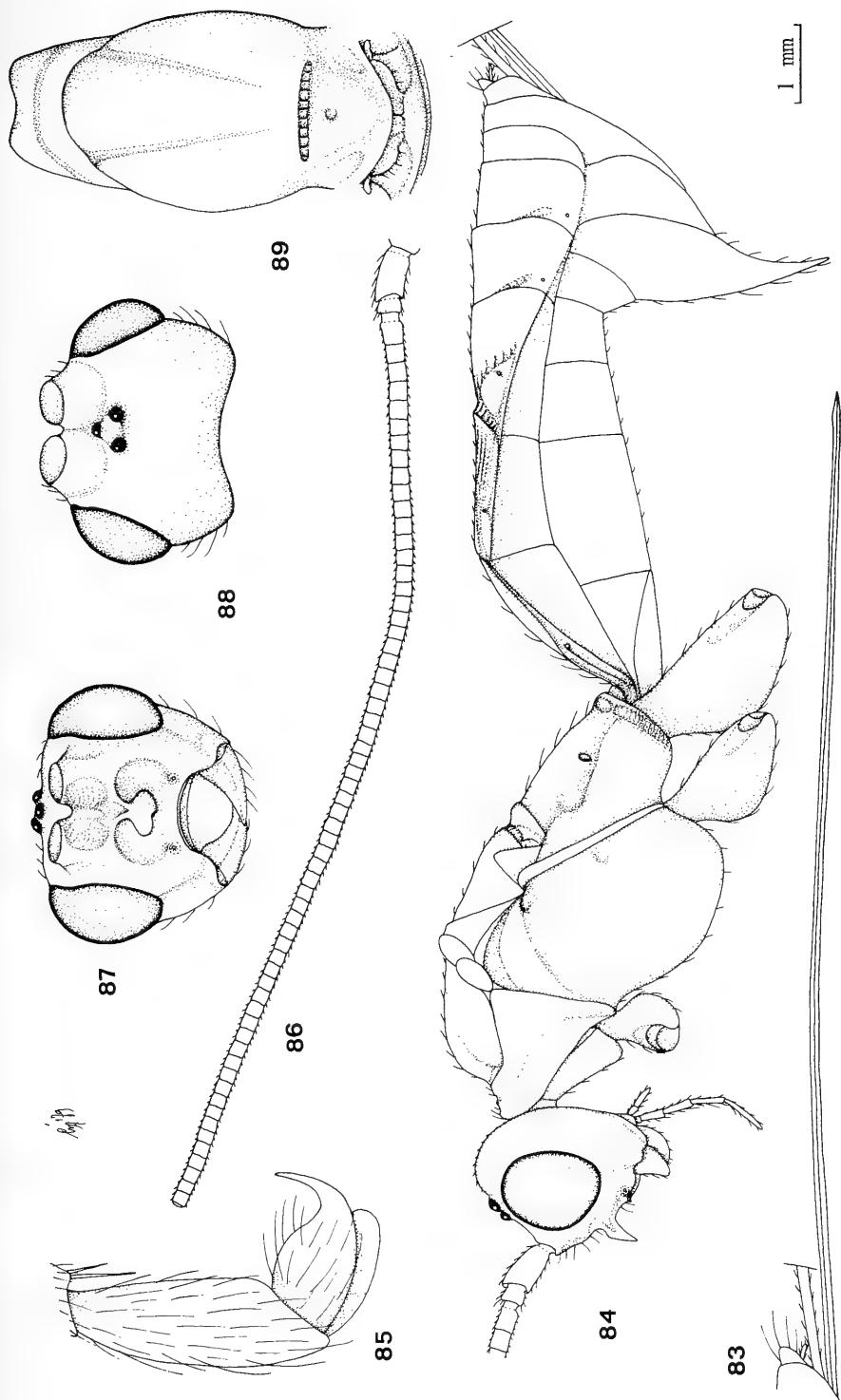
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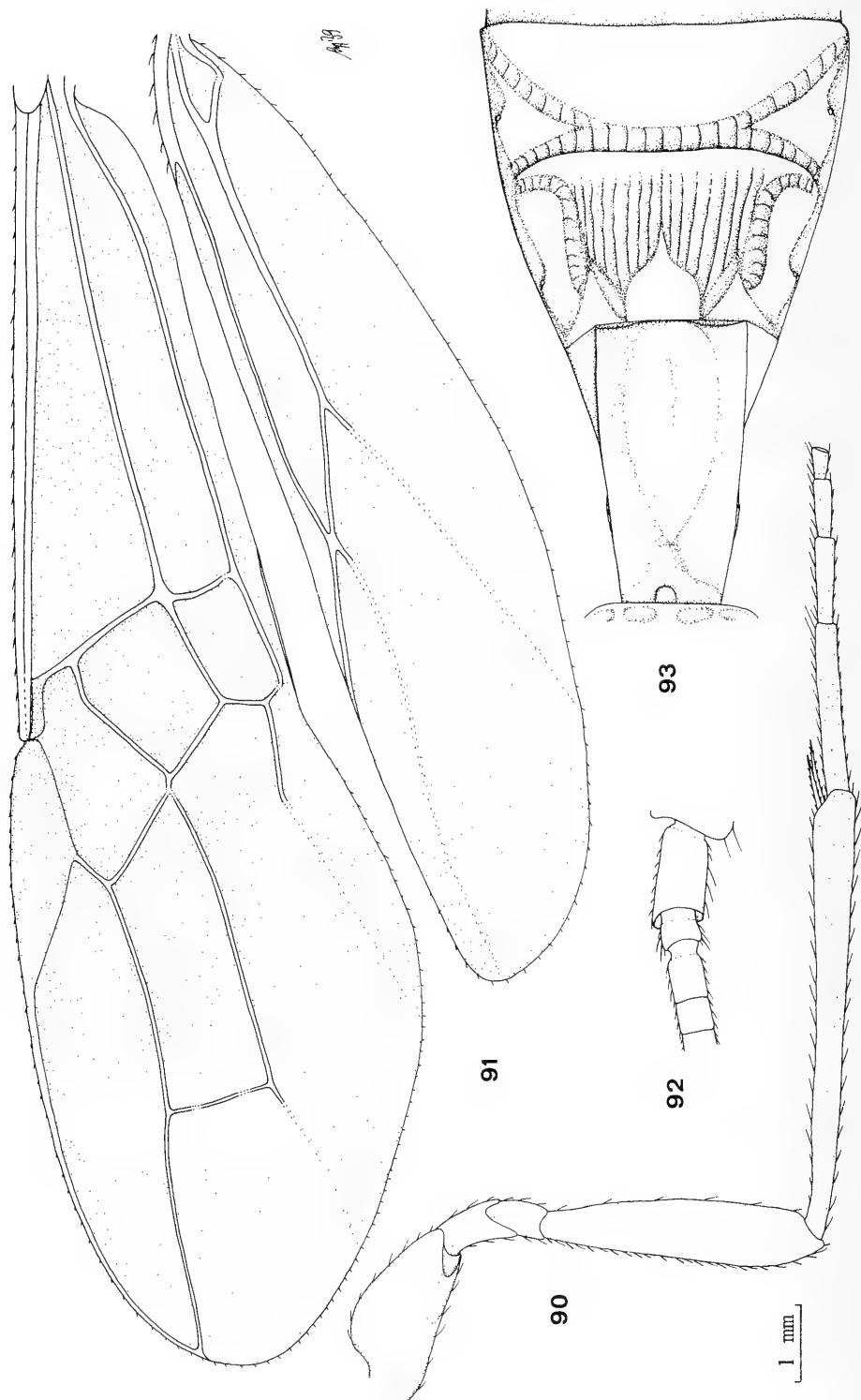
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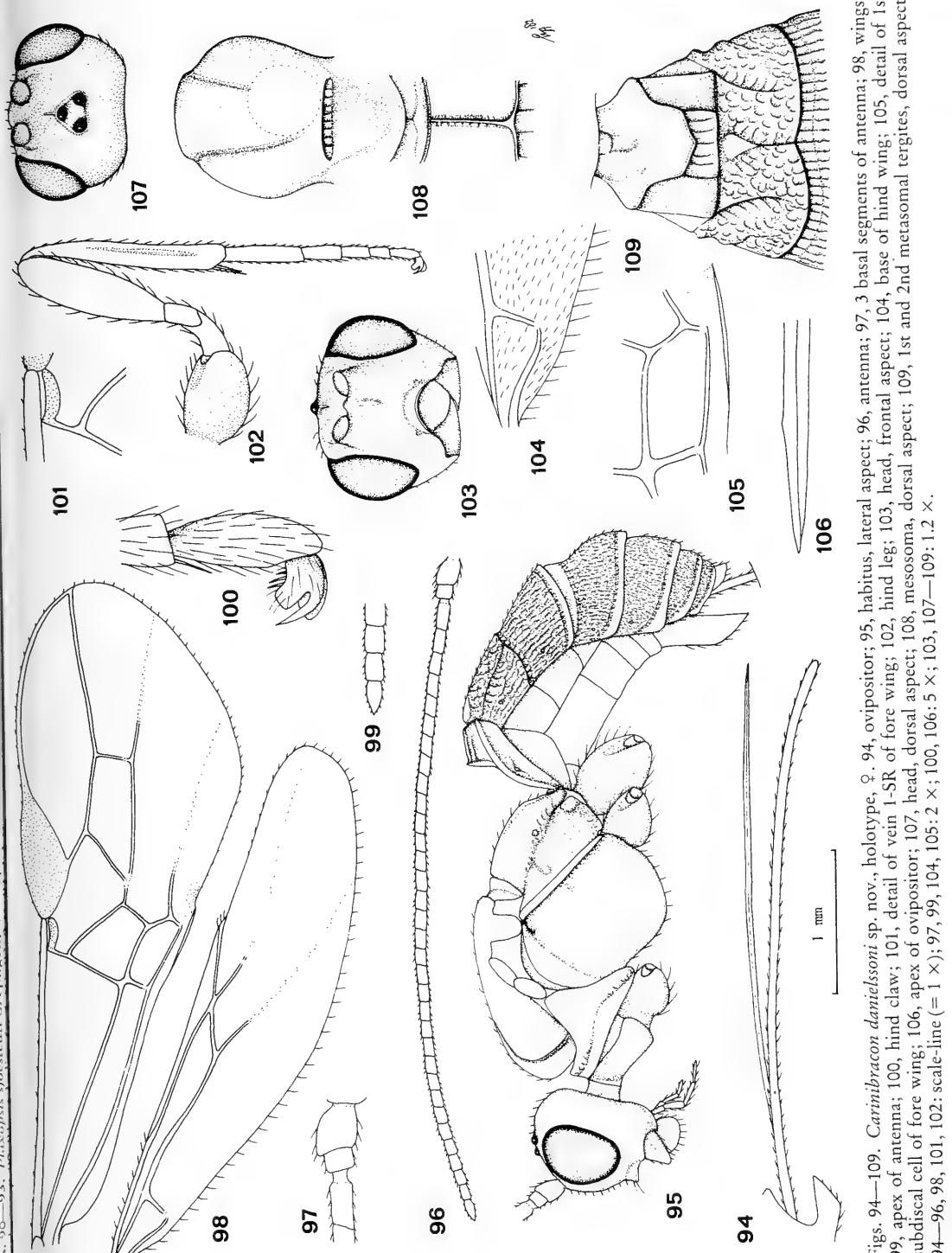
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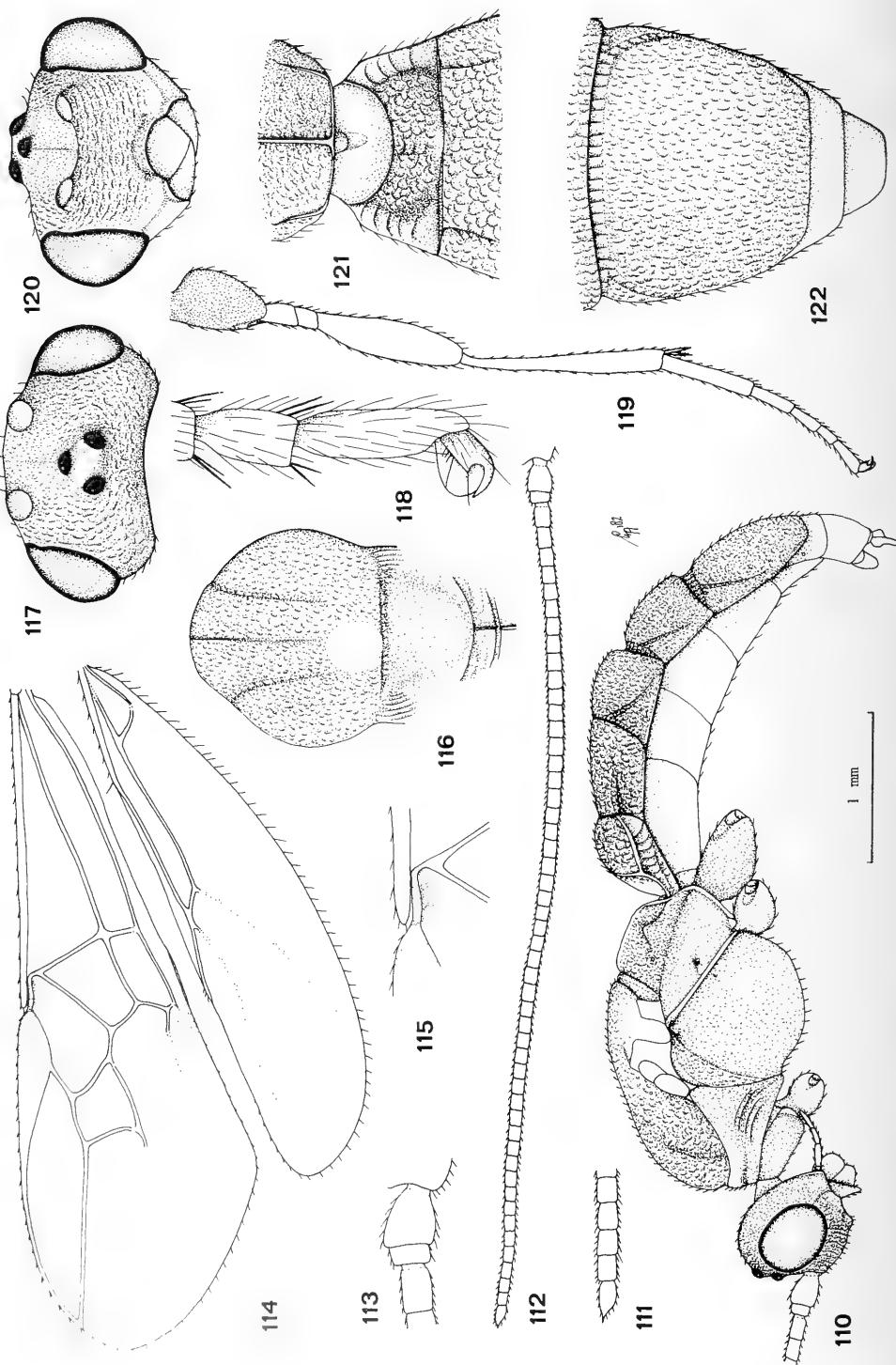
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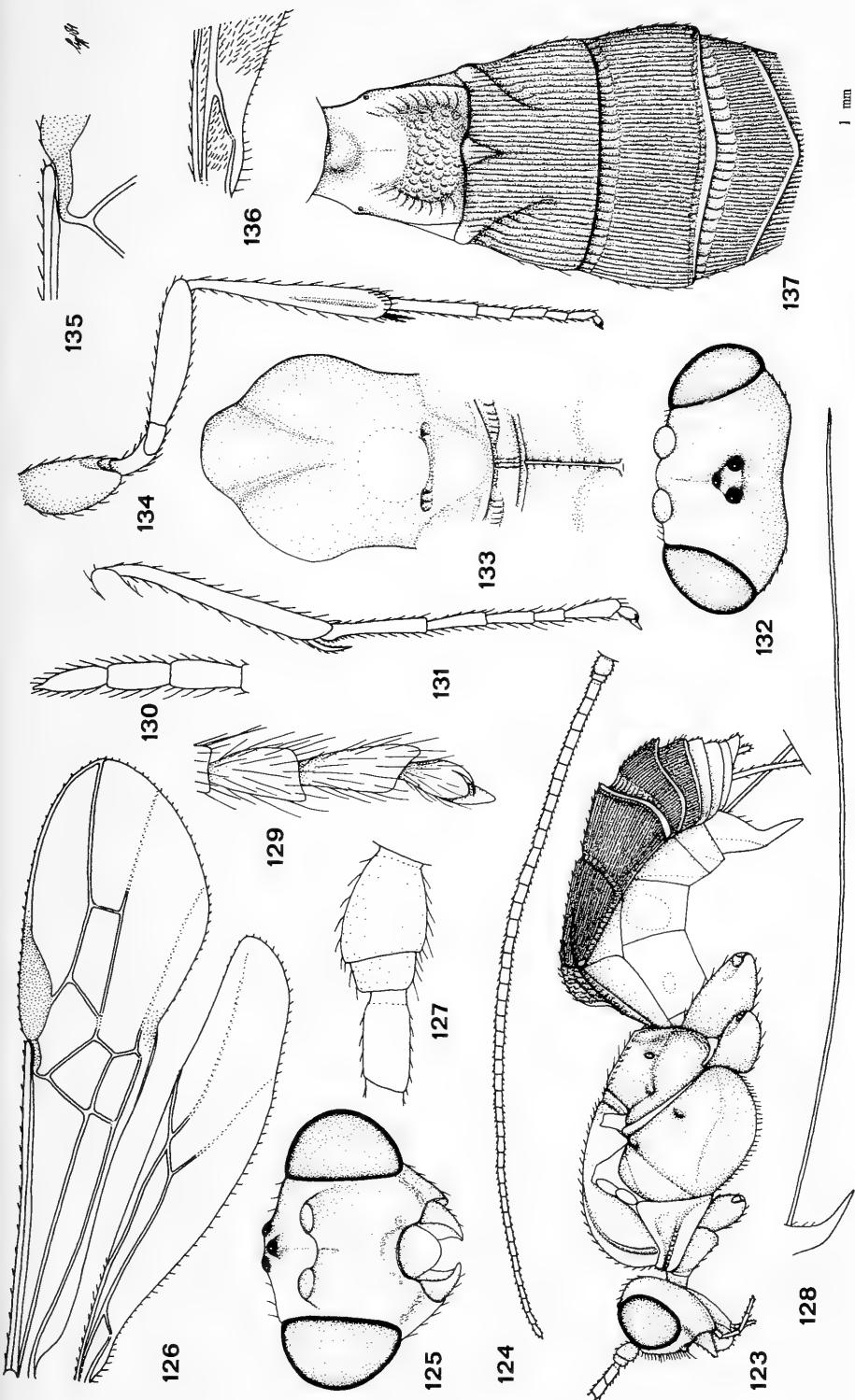
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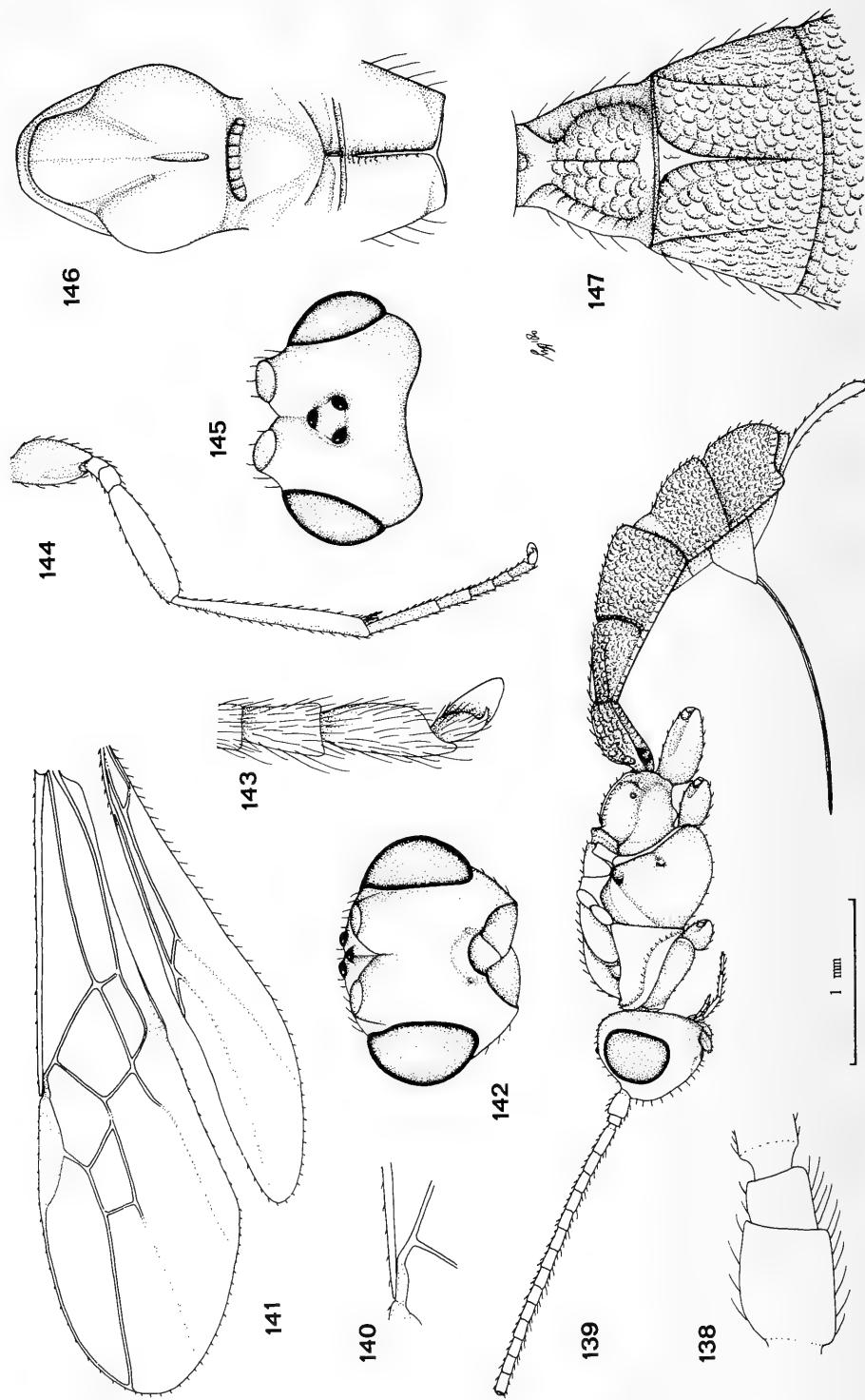
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Figs. 138—147. *Adesa albolineata* Cameron, holotype, ♀. 138, scapus, outer aspect; 139, habitus, lateral aspect; 140, detail of vein 1-SR of fore wing; 141, wings; 142, head, frontal aspect; 143, hind claw; 144, hind leg; 145, head, dorsal aspect; 146, mesosoma, dorsal aspect; 147, 1st and 2nd metasomal tergites, dorsal aspect. 138, 143: 5 X; 139, 141, 144: scale-line (= 1 X); 140, 142, 145—147: 2 X.

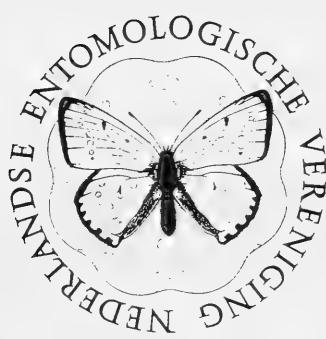




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L. BRUSSAARD. — Reproductive behaviour and development of the dung beetle *Typhaeus typhoeus* (Coleoptera, Geotrupidae), pp. 203—231, figs. 1—17.



# REPRODUCTIVE BEHAVIOUR AND DEVELOPMENT OF THE DUNG BEETLE *TYPHAEUS TYPHOEUS* (COLEOPTERA, GEOTRUPIDAE)

by

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The Netherlands*

## ABSTRACT

This paper is part of a study of the contribution of dung beetles to soil formation in sandy soils. *Typhaeus typhoeus* (Linnaeus) has been selected because it makes deep burrows and is locally abundant. The beetles are active from autumn until spring, reproduction takes place from February to April. Sex pheromones probably influence pair formation. The sexes co-operate in excavating a burrow (up to 0.7 m below surface) and in provisioning the burrow with dung as food for the larvae. Co-operation is reset by scraping each other across the thorax or elytra. Dung sausages, appr. 12.5 cm long and 15 mm in diameter, are manufactured above each other. Development is rapid at 13–17 °C. The life cycle is accelerated by a cold period in the third larval stage. These requirements are met by soil temperatures up to 15 °C in summer and down to 5 °C in winter. The life cycle lasts two years, but longer under certain conditions. Newly hatched beetles make their way to the surface through the soil, but do not follow the old shaft. Adults reproduce only once. Differential rate of completion of the life cycle and occasional flying probably reduce the risk of local extinction. The study is thought to be relevant for behavioural ecology and soil science.

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## INTRODUCTION

There were two main reasons for this study of dung beetles. First, ancient traces of former activity by small burrowing or crawling animals, presumed to be dung beetles, can be found today in sandy soils. By studying the behaviour of dung beetles it should be possible to ascertain whether these are indeed the relics of dung beetle activity.

Second, in areas where dung beetles are abundant nowadays, recent traces of their activity are present in the soil and this raises the ques-

tion of how much dung beetles contribute to soil formation today.

These topics will be discussed in subsequent articles. The ancient traces (with an account of their age) will be described in a forthcoming paper and will be compared with the traces resulting from recent dung beetle activity. It will be shown that dung beetles may indeed be responsible for the ancient traces.

Knowledge about the reproductive behaviour of the dung beetles is required for a proper understanding of their influence on soil morphology, and therefore this is discussed in the present paper. After a brief introduction to dung beetles as a group, the general biology of the species selected for study, i.e. *Typhaeus typhoeus* (Linnaeus, 1758), is described and its geographical range is discussed.

In order to quantify the beetles' contribution to soil formation it will eventually be necessary to explain and predict their population dynamics. This considerable task was reduced to two basic investigations in the present study. The first pertains to the development of life stages during the season and to phenological phenomena that seem to be related to the persistence of

the species in time and space. As this constitutes part of the biology of the species it has been included in the present paper. The second basic investigation pertains to the environmental conditions (including soil conditions) with which the beetles have to cope during the season of adult activity. These conditions may affect the beetles' burrowing and reproduction. This will be treated in another paper. It will be shown that the number of dung targets and their distribution in the field is of paramount importance for the population ecology of *T. typhoeus* and its impact on soil.

In its impact on soil *Typhaeus typhoeus* should serve as a model species for all Geotrupini found in the temperate Holarctic and, to some extent, also for other dung beetle species of the paracoprid type in other parts of the world.

Consequently, in this paper about *T. typhoeus*, the emphasis will be on aspects of behaviour that may help to explain the impact on soil formation caused by this kind of dung beetle. Aspects of the reproductive behaviour of *T. typhoeus* that have been published elsewhere will be re-described in terms of their relevance to soil formation. Furthermore, useful new information about behaviour and the development of life stages will be presented.

#### DUNG BEETLES AND THEIR ASSOCIATION WITH SOIL

Representatives of several coleopteran families are regularly found inhabiting dung, e.g., Hydrophilidae and Histeridae. The term "dung beetle", however, is usually restricted to a number of species belonging to the superfamily Scarabaeoidea. Scarab beetles, whether dung beetles or not, show a close connection with soil. The larvae of most species live underground on a food-stock of dung or plant remains, prepared by their parents, or they show a free-living, root-sucking habit. Adults of most species forage above-ground on fungi, dead organic matter or fresh leaves and burrow into the soil to prepare food-stocks for their larvae, to lay eggs or to hibernate or aestivate.

Living on dung may have evolved from living on dead organic matter and fungi (Iablokoff-Khnzorian, 1977; Crowson, 1981). In the family Geotrupidae, to which *Typhaeus typhoeus* belongs, all these habits occur and this family has been placed near the base of the scarabaeoid evolutionary tree by the authors mentioned above. Dung-feeding beetles may have devel-

oped the practice of digging into the soil as a result of searching for truffle-like fungi that adopted a subterranean life history during times of warming climate. The habit of making food-stocks out of dead organic matter or dung instead of searching for fungi is presumed to have developed subsequently.

Dung beetles spread all over the world from the Jurassic/Cretaceous periods onwards (Iablokoff-Khnzorian, 1977; Crowson, 1981). The Geotrupini tribe probably radiated out from the area of the Tertiary Tethys Sea (Krikken, 1980) and now shows a predominantly temperate, Holarctic distribution.

In addition to the Geotrupidae, one other family of scarab beetles is important for our study, viz., the Scarabaeidae. This family not only contains dung beetles (e.g. Scarabaeinae and Aphodiinae), but also beetles of the cockchafer type (Melolonthinae), which, as adults, live on fresh leaves and, as larvae, show a root-sucking way of life. Cockchafers will be discussed in a subsequent paper.

#### CHOICE OF *TYPHAEUS TYPHOEUS* AS AN OBJECT OF STUDY

The impact of dung beetles on soil may be two-fold: enrichment with dung or plant remains, and physical disturbance. On the basis of their impact on soil, dung beetles may be divided into three ecological groups, as proposed by Bornemissza (1969) in a different context.

First, the endocoprids, which pass their life cycle from egg to adult in the dung on the surface, or spend part of their life cycle a few centimetres deep in the soil, e.g. Scarabaeidae-Aphodiinae. Second, the telecoprids, which make a ball out of the dung, roll it some distance away and bury it superficially as a food source for the larva, e.g. Scarabaeidae-Scarabaeinae. And, third, the paracoprids, which burrow a fairly deep shaft under or close to the dung patch; part of the burrow is filled with food for the larvae and part of it is back-filled with soil, e.g. Geotrupidae.

Because of the depth of the shafts and the amount of dung transported below the ground, dung beetles of the paracoprid type, especially the larger species, may be considered to have the greatest impact on soil. In the temperate regions, paracoprid dung beetles of the Geotrupini tribe are the most important in this respect, as has been shown by the studies of Fabre (± 1910), Schreiner (1906), Spaney (1910), Von Lengerken (1954), Howden (1955, 1964, 1974),

Table 1. Depth of shafts in Geotrupidae.

faunal region	species	depth of shaft (cm)	source
Palaearctic	<i>Geotrupes mutator</i> *	≤ 30	Teichert, 1955
	<i>G. spiniger</i> *	25—30	Lumaret, 1980
	<i>G. stercorarius</i> *	≤ 50	Teichert, 1955
		35—60	Spaney, 1911
	<i>G. stercorosus</i> *	35—60	Spaney, 1910
	<i>G. vernalis</i> *	12—68	Teichert, 1959a
	<i>Lethrus apterus</i>	60—100	Frantsevich et al., 1977
		75—100	Teichert, 1959b
		50—65	Schreiner, 1906
	<i>Typhaeus momus</i>	10—15	Baraud, 1977
	<i>T. typhoeus</i> *	29—100	present study
		60—100 (150)	Kuyten, 1960
		48—130	Teichert, 1959b
		70—140	Spaney, 1910
Nearctic	<i>T. biostius</i>	≤ 150	Fabre, ca. 1910
	<i>Geotrupes egeriei</i>	60—160	Crovetti, 1971
	<i>G. hornii</i>	20—75 (90)	Howden, 1955
	<i>Bolboceras farctum</i>	40—75	id.
	<i>Bradykinetus ferrugineus</i>	57	id.
	<i>Mycotrupes retusus</i>	35—105	id.
	<i>M. gaigei</i>	45—90	Olson, Hubbell & Howden, 1954
	<i>Peltotrupes youngi</i>	≤ 205	id.
		140—270	Howden, 1952

\* occurring in The Netherlands.

Teichert (1955, 1956, 1957, 1959a), Kuijten (1960), Crovetti (1971) and Klemperer (1978, 1979). There are differences between geotrupid species in, for example, geographical range, habitat, (use of) flight capability, reproductive season, depth of the shaft (table 1) and number of eggs laid (table 2).

In northwest Europe, *Typhaeus typhoeus* (fig. 1) is one of the most obvious species to study. The beetles are locally abundant with a

maximum of 1—2 pairs per m<sup>2</sup> and they make very deep burrows (tables 1 and 3). Occasionally I have found them as deep as 1 m and they may go even deeper, up to 1.50 m (Fabre, ± 1910; Spaney, 1910; Teichert, 1959b; Kuijten, 1960). Moreover, they transport a fair amount of dung below the ground, as reflected by the number of dung sausages produced (= number of eggs laid; tables 2 and 4).

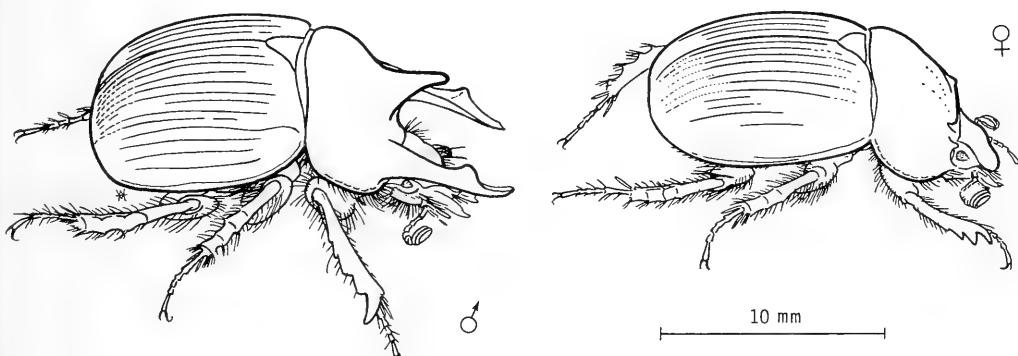


Fig. 1. *Typhaeus typhoeus* (Linnaeus, 1758). Left, male, and right, female.

Table 2. Number of eggs laid per nest or per female (if reported) in Geotrupidae.

species	number of eggs laid per nest or per female	source
<i>Geotrupes mutator</i> *	4—16 per ♀	Teichert, 1955
<i>G. spiniger</i> *	9—10 per ♀	Lumaret, 1980
<i>G. stercorarius</i> *	4—17 per ♀	Teichert, 1955
	(2) 3—6 (8)	Spaney, 1910
<i>G. vernalis</i> *	5—10 per ♀	Teichert, 1959a
<i>Lethrus apterus</i>	5—7	Frantsevich et al., 1977
	6—11 per ♀	Schreiner, 1906
<i>Typhaeus typhoeus</i> *	(1) 4—16 (21) per ♀	present study
	1—6 per nest (field)	id.
	≤ 10 per nest	Palmer, 1978
	≤ 15 per ♀	Kuyten, 1960
	3—6 (8)	Spaney, 1910
<i>T. biostius</i>	2—8 per nest (field)	Crovetti, 1971

\* occurring in The Netherlands.

## GENERAL BIOLOGY

### Nesting

The reproductive behaviour consists of burrowing a branching shaft, provisioning the branches with food for the larvae and sealing the remaining burrow partly or completely with soil. Though the female, once fertilized, can perform the whole process on her own, the beetles normally operate in pairs. Some aspects of the reproductive behaviour have been outlined previously by Fabre (± 1910), Kuyten (1960) and Palmer (1978).

### Habitat

The habitat is open to half open heathland, and the beetles are most abundant in bare areas surrounded by *Nardus stricta*, *Cladonia* spp. and *Calluna vulgaris*, and along paths. They also occur in open pine woods, predominantly along paths and in small clearings. A vital prerequisite is the presence of dung. The beetles are found only on herbivore dung, mostly that of rabbits, as the rabbit is the most abundant herbivore in the habitat of *T. typhoeus*. They will also use dung from sheep, deer and roe.

### Seasonal and diurnal incidence

From the second half of September onwards and throughout the winter, *T. typhoeus* is active whenever the temperature is above zero and there is no snow. Intense activity occurs in October and November, which is the main period of maturation feeding, and from February to April, which is the main period of reproduction. From May onwards the reproductive activity

declines rapidly and from June to the latter half of September there is no adult activity at the soil surface (fig. 2). Contrary to the common assumption that the beetles only reproduce after the turn of the year (Fabre, ± 1910; Main, 1917; Kuijten, 1960) I have established from field observations that pair formation, oviposition and provisioning with dung is not exceptional as early as the third week of October. On the other hand, unpaired beetles can be found in shallow burrows as late as March, where they are apparently still involved in maturation feeding.

Although in overcast and humid weather activity on the surface by day is not exceptional, *T. typhoeus* is usually active above-ground at dusk and at night.

## DISTRIBUTION

### The genus *Typhaeus*

The genus *Typhaeus* Leach, 1815, contains six species of about the same size: 14—22 mm long and 8—11 mm wide. Five of these are restricted to the Mediterranean area: *T. biostius* (Gené, 1836), *T. momus* (Olivier, 1789), *T. fessor* (Waltl, 1838), *T. lateridens* (Guérin, 1838) and *T. typhoeoides* Fairmaire, 1852. The first of these is endemic to Sardinia. The sixth species, *T. typhoeus* has the largest geographical range: from Morocco to South Sweden, westwards to Ireland and eastwards to Poland (Horion, 1958; Lindroth, 1960) and Yugoslavia (Miksić, 1956), but it is absent in Hungary (pers. obs. and Endrödi, pers. comm., 1981). A preliminary map of the distribution in Europe is given in fig. 3.

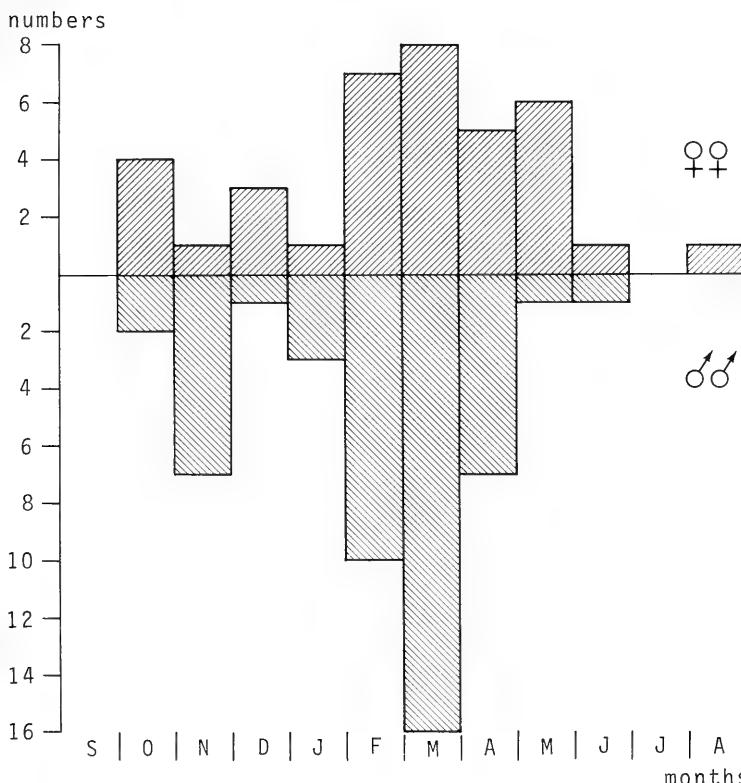


Fig. 2. Number of *Typhaeus typhoeus* captured in standard pitfalls in various heathlands in the Dutch province of Drenthe during the years 1959—1967. (Courtesy of P. J. den Boer.)

### *Typhaeus typhoeus* in The Netherlands

In The Netherlands, *T. typhoeus* is found in sandy areas, even in isolated spots surrounded by peat, clay or loam soils (Gaasterland, Betuwe, South Limburg) but, remarkably, it is not present in the dunes along the west coast and on the Wadden islands in the north of the country. Fig. 4 is a preliminary map of the distribution of *T. typhoeus* in The Netherlands.

### Absence from the dune region

In a preliminary experiment to ascertain the reasons for the absence of *T. typhoeus* from the dunes, it was found that under laboratory conditions two pairs of beetles reproduced quite normally when supplied with pellets of rabbit dung from the Wadden island of Vlieland. The trial was stopped when the larvae were in their final instar. Under field conditions in enclosures in the dunes of North Holland near Castricum, beetles made normal burrows in which they

provisioned dung for their offspring, whether supplied with pellets of rabbit dung from the dunes (two pairs) or from the inland (two pairs). When the burrows were excavated six months later, it appeared, however, that only one of the 22 dung sausages contained a live larva, whereas in most of the other cases the larva had died and in some cases the egg had evidently not hatched. This work needs to be continued to yield conclusive results.

### METHODS

To study the behaviour of *T. typhoeus* in the laboratory, the beetles were kept in cages (1 m high and 0.60 m wide), similar to the one described by Main (1916/17): a wooden frame in which two windows (4 mm thick) were kept a distance of 15 mm (sometimes 12 mm) apart. The space between the windows was filled from above with tamped down portions of sand that came from a field at Wijster, in the Dutch prov-

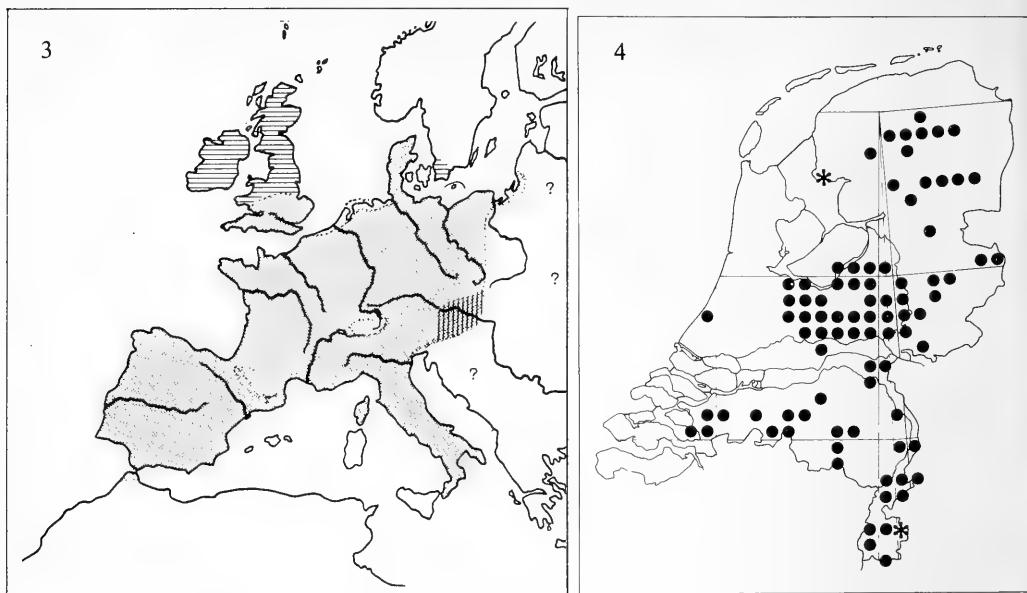


Fig. 3. Geographical range of *Typhaeus typhoeus*. Grey area: after Pijpers (1981). Striped area: *typhoeus* present according to Horion (1958), Lindroth (1960) and Sinclair (1977). Barred area: *typhoeus* not occurring according to Endrödi (pers. comm., 1981).

Fig. 4. Distribution of *Typhaeus typhoeus* in The Netherlands. After Pijpers (1981). Each dot indicates at least one specimen. Stars constitute additional occurrences, assessed by present author. The dot near the west coast pertains to two specimens, captured around the turn of the century.

ince of Drenthe, where *T. typhoeus* occurs naturally. The soil there is coversand to a depth of 1.40 m, in which a podzol has developed (Van Heuveln, 1965). The predominant particle size was 0.1—0.2 mm and particles larger than 0.6 mm were scarce. The organic matter content of the sub-soil was 0.6%. The sand was air-dried and subsequently moistened to a water content of 10% (by mass) to approximate field conditions in September at a depth of about 0.50 m below the surface. The tamping resulted in a bulk density of approximately 1.50 g/cm<sup>3</sup>, which was similar to the field situation at about 0.50 m below the soil surface.

The beetles made their burrows in the sand between the windows. The light/dark regime in the rooms with the cages was the same as in nature. Daylight conditions were simulated with TL-33 tubes supplemented with normal bulbs. To prevent light affecting the beetles in the soil, the windows of the cages were covered with sheets of black plastic. A horizontal walking-surface (0.50 × 0.60 m<sup>2</sup>) on which dung could

be offered was mounted on top of the glass cage and covered with 0.8 mm mesh wire-netting to prevent the beetles from flying away. Observations were usually carried out under dim red light, after the plastic sheets had been removed.

For the rearing 60 cages were used. To compare the laboratory results with the field situation, five cages were dug into the soil in the field at Wijster. In addition, the experimental equipment in the field included five 1 × 1 m<sup>2</sup> and six 2 × 2 m<sup>2</sup> enclosures consisting of 0.50 m wide stainless steel plates which were inserted to a depth of 0.20 m in the soil. These enclosures were also spanned with the wire-netting.

Almost all beetles used in the experiments were captured at the same site near Havelte in the province of Drenthe. Newly hatched adults can easily be collected in autumn from under the small hummocks of soil, where they have retired with some dung for their maturation feeding. Prior to experiments the beetles were kept in sand-filled plastic jars, 13 cm high and 10 cm in diameter, for a least six weeks at 5 °C.

Further details about the experimental methods will be given in the appropriate sections below.

#### REPRODUCTIVE BEHAVIOUR

##### Emergence and maturation feeding

The first newly hatched adults of *T. typhoeus* appear on the surface in the second half of September, usually after heavy rain. They immediately go in search of dung.

As soon as a beetle has found a small collection of dung it excavates a J-shaped feeding burrow approximately 15–20 cm deep (in the case of females sometimes deeper) and 13–16 mm in diameter. The beetle carries a number of dung pellets (in the case of rabbit dung mostly 10–20) down into its burrow and starts its maturation feeding. Given that reproduction was observed as early as the third week of October, the maturation feeding time in *T. typhoeus* is probably approximately four weeks, at a temperature of 13–16 °C.

##### Flying

To judge from the many beetles I found crawling around on the surface and the relatively few flying, it would seem that the beetles mostly move by walking and less so on the wing. Nonetheless, flying was observed in the field at a temperature of about 12 °C in the second week of October at dusk, in foggy weather with little wind. The beetles emerged from their burrows with their hind wings already unfolded and pumped up and flew off immediately. They flew low, zigzagging over the vegetation and the maximum distance I saw covered in one

flight did not exceed an estimated 50 m. Attempts to fly were also observed at the same time of the day in the laboratory in the plastic jars in which the beetles were kept prior to experiments. Blut (1938) encountered *T. typhoeus* flying at dusk in late May. Flying is possible even at very low temperatures, since in one of my laboratory experiments a female flew around in the walking area of a glass cage at 5 °C, although she had been subjected to that temperature for over six weeks.

To study flight movements in *T. typhoeus* more closely, two window traps and a mist-net trap were placed in a study plot at Wijster, in the Dutch province of Drenthe. The window of the window trap measures 100 × 50 cm<sup>2</sup> and it catches beetles flying at a height of 150–200 cm above the ground. The mist-net trap measures 100 × 50 cm<sup>2</sup>, catching beetles flying 20–70 cm above the ground. After colliding with a trap the beetle falls down into a reservoir containing 4% formaline. The two window traps were in operation from 29 September 1978 and the mist-net trap from 8 November 1978 until the summer of 1980. In all, 19 beetles were trapped: eight males and eleven females (fig. 5). Fifteen beetles were captured in the single mist-net trap and only four in the two window traps, which confirms that the beetles fly low. Of the eleven females, ten were relatively unimpaired when the trap was inspected; two (captured on 27 September and 1 October, respectively) showed developing ovaries and had not yet mated; eight contained eggs and had mated, to judge from the presence of sperm cells. This shows that although no flying beetles were captured during peak reproduction in March, *T. typhoeus* can be

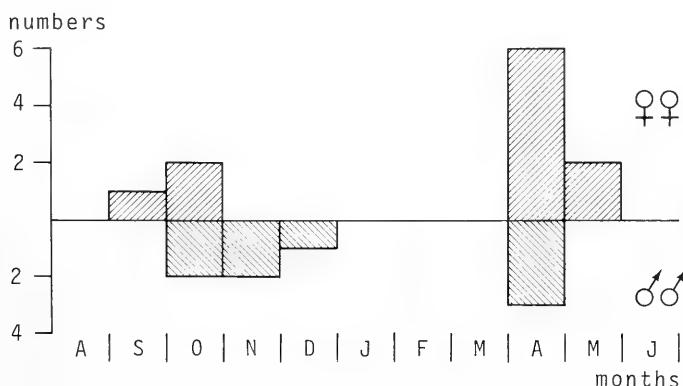


Fig. 5. Number of beetles trapped in flight at a study plot at Wijster (province of Drenthe, The Netherlands) during 1978/79 and 1979/80.



Fig. 6. Stance adopted by male *Typhaeus typhoeus* for supposed pheromone release during defecation. (Photo of beetle in nest entrance on walking surface of glass cage.)

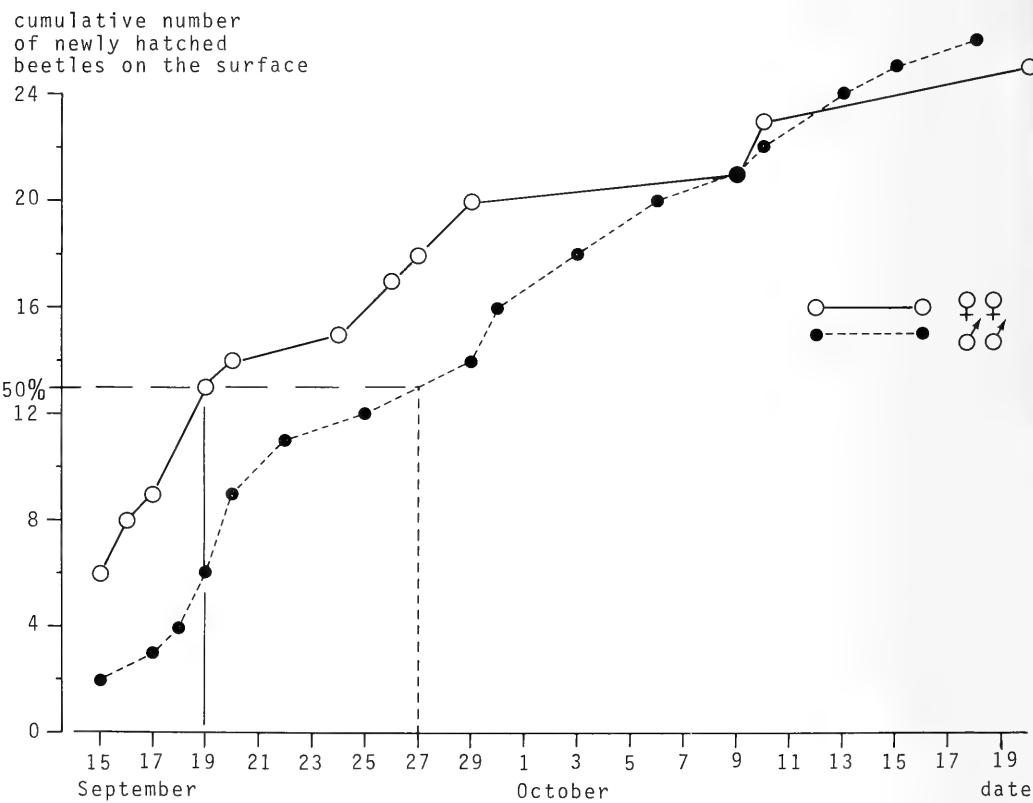


Fig. 7. Cumulative number of newly hatched male and female beetles appearing at the surface in September and October 1980 in a rearing trial started in late winter 1979.

added to the list of species not obeying the oogenesis-flight syndrome of Johnson (1969).

The gut content of 14 of the trapped beetles was qualitatively estimated. In five beetles the gut was half filled or less, in nine the gut was more than half full. From these findings it cannot be concluded that a shortage of dung is the reason for flight.

#### Settlement and pair formation

Crovetti (1971) states that in *Typhaeus hios-tius* the male penetrates the feeding burrow of a female after maturation feeding. In *T. typhoeus* I have observed behaviour that strongly suggests that pheromones may play a role, at least

in some stage of adult life, in pair formation: under laboratory conditions I have repeatedly observed that a male who has abandoned a nest with a female, then digs a shallow burrow near a food source, similar to the J-shaped feeding burrow. Next to this the male can be observed defecating in a characteristic stance, his body tilted at an angle of about 45° to the surface with his head above the entrance of the burrow and his abdomen lifted (fig. 6). This stance suggests that a pheromone is released with the excrement. Although the hypothesis of pheromone release needs experimental confirmation, it is significant that this stance was invariably adopted around the time that the light in the ex-

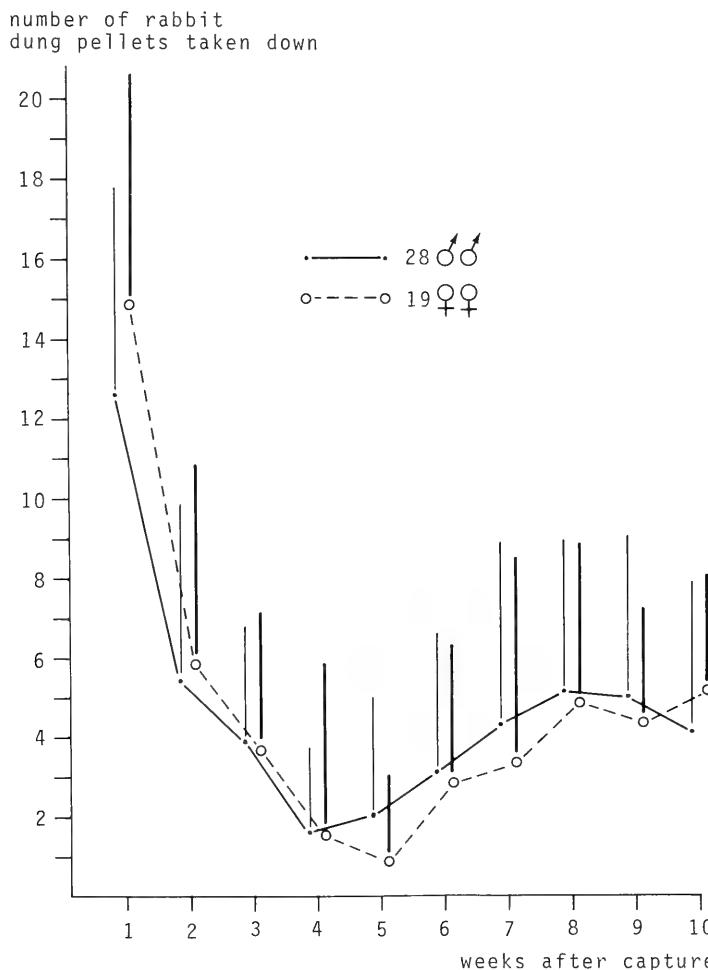


Fig. 8. Mean number of rabbit dung pellets carried down by beetles kept in plastic jars at 13—16 °C for ten weeks after their capture on 29 September and 4 October 1978. Vertical lines indicate upper half of standard deviation.

perimental room was automatically switched on or off, i.e., around dawn or dusk. At those times the weather is usually favourable for odour communication because of high air humidity and moderate wind velocity.

Crovetti's (1971) observation that the male joins the female after maturation feeding and my observation that males appear to be trying to attract females after the pair has split up, suggests that the former behaviour changes to the latter in the course of the season (assuming the two *Typhaeus* spp. behave similarly). There is some evidence to support this. In the rearing trials I carried out, the females usually appeared on the surface and started maturation feeding before the males: the median of the total number of females on the surface was reached eight days before that of males (fig. 7). Furthermore, in a cohort of beetles captured in the field, females carried down the same quantity of dung for maturation feeding as did the males (fig. 8). If the duration of maturation feeding is the same for both sexes then it seems probable that females mature sexually earlier than the males. For a female, the prerequisites for reproduction are a male and an adequate amount of dung, as a food source for the future larvae, and therefore her most profitable strategy seems to be not to go and search for one of the few males available for mating, but rather to settle near a spot rich in dung, make a shallow burrow and wait there for a male. This needs to be confirmed by additional research.

During the reproductive season the pattern changes: whenever a pair of beetles abandons a nest it is usually the male who leaves first, as will be reported in greater detail in another paper. Several days may pass before the female appears outside the burrow. By the time the male leaves the burrow most females will be paired and involved in breeding, so that it is unprofitable for him to search for one of the few burrows with an unpaired female. Instead, he seeks a spot with plenty of food, near which a new nest can be made, and tries to attract one of the females that will appear above-ground after abandoning a nest.

### Copulation

On the first encounter, which usually takes place in a shallow feeding burrow, the male vigorously sweeps his front tibiae across the female's thorax, the female turns around and then the male sweeps across her elytra while half

mounted on her back. Finally, the female lifts her abdomen and copulation follows, lasting from 3 to 20 min. The female terminates the copulation by stepping forwards a few cm, turning around and pushing the male back.

### Burrowing

Having paired and copulated the beetles make a nest that finally consists of a shaft that may or may not divide into tunnels, from which a number of brood chambers branch off, provisioned with dung for the progeny and sealed by back-filling with soil (fig. 9). The female excavates by scraping the sand under her body with her front tibiae and then using her middle and hind legs to move it further back. As the sternites are densely covered with backward-pointing hairs, the sand does not fall down past the beetle when she is in a vertical position. While excavating, the beetle intermittently turns around its length axis. Every time the beetle has excavated 0.5—1.0 cm of the shaft she moves several mm backwards, and by doing this tamps down the moist sand behind her into a plug. Then she turns around and pushes the plug into the shaft with her head and thorax, again intermittently turning around her length axis. This turning enables her to apply force to a different point and thus facilitates the transport of the plug. The upper part of the shaft, within a depth of 30 cm from the surface, is made horizontal for some 10—15 cm (fig. 9). Here the female always leaves her sand plug before returning down the burrow to continue excavating. The male then burrows through the sand plug. Since the female has left the plug in a horizontal part of the passage, the sand does not fall down the shaft. Once past the small plug, the male turns around and shovels it to the exit, transporting it in the same way as the female. In this way a sand heap gradually accumulates on the surface, finally achieving a height of some 5 cm and a diameter of 10—15 cm.

In one of the glass cages the excavation of the shaft was closely monitored. Fig. 10 clearly shows that the beetles may continue to excavate for four days without pausing.

On four successive days, during periods indicated in fig. 10, I recorded the intervals during which the female was involved in sand excavation and transport, respectively. On the first three days the duration of the periods of excavation was the same, on the fourth day the duration was much longer, presumably indicating that the female was about to terminate the bur-

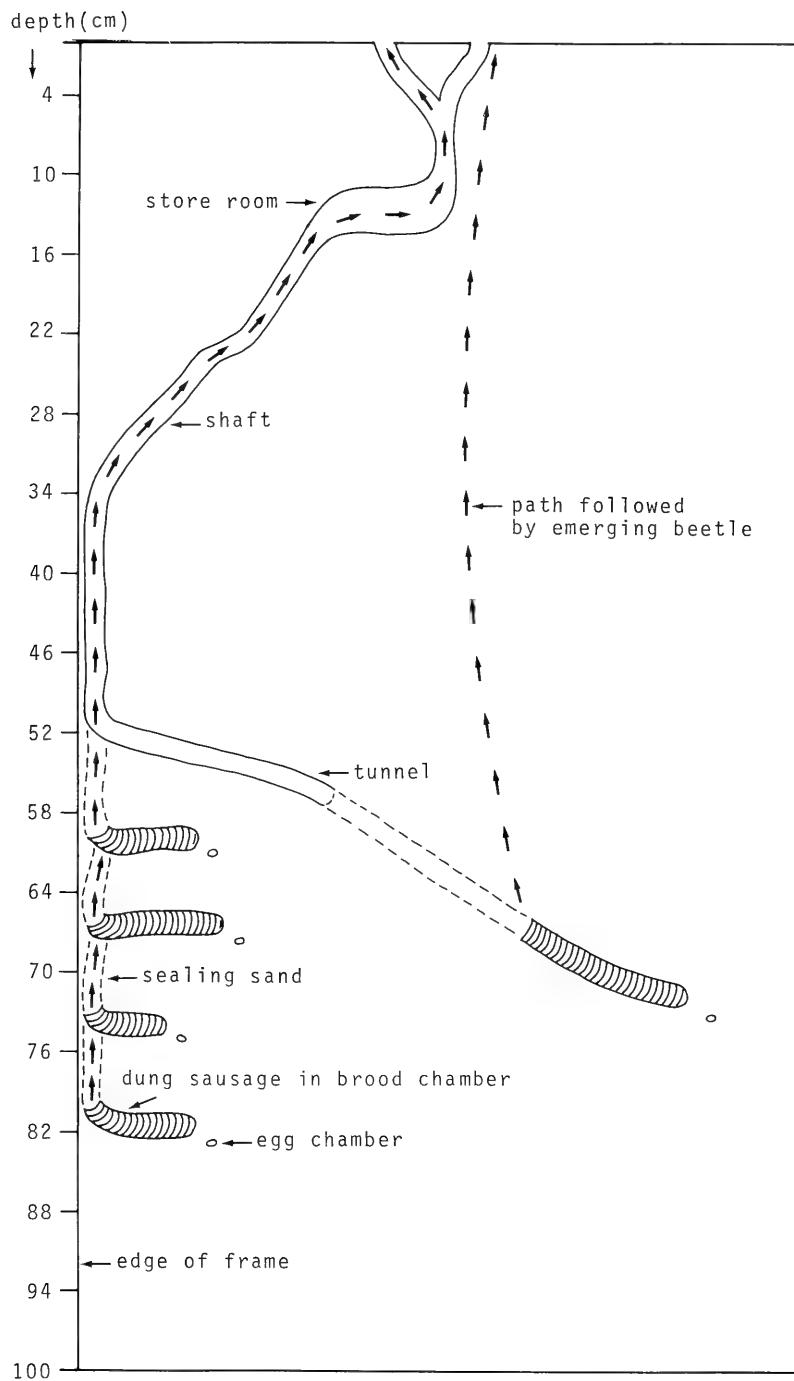


Fig. 9. Nest of *Typhaeus typhoeus* in one of the glass cages.

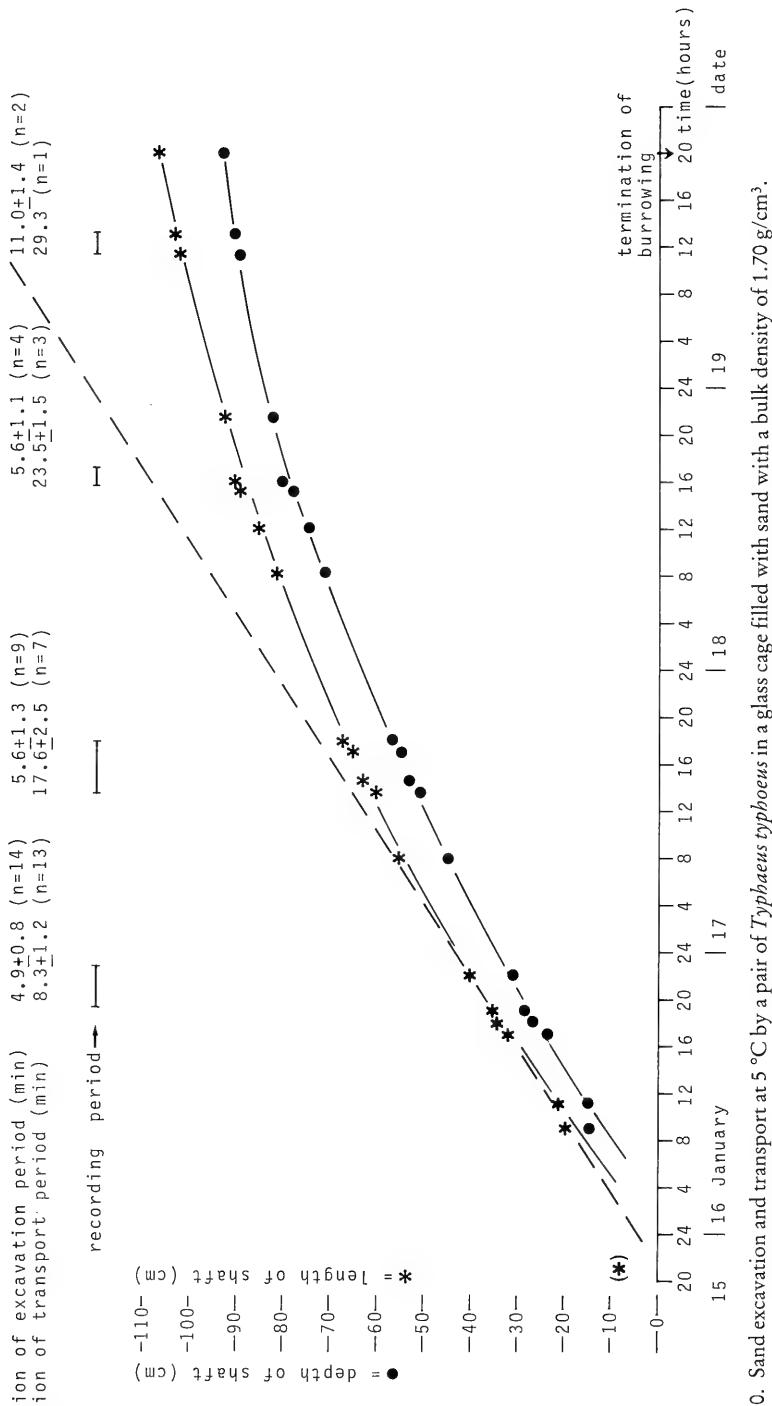


Fig. 10. Sand excavation and transport at 5 °C by a pair of *Typhaeus typhoeus* in a glass cage filled with sand with a bulk density of 1.70 g/cm<sup>3</sup>.

rowing. The duration of sand transport steadily increased to half an hour per plug. The cage had been filled and the sand tamped down under water. This resulted in a bulk density of 1.70 g/cm<sup>3</sup>, which is the maximum a beetle may generally encounter in the field. The temperature in the room with the cage was 5 °C throughout the reproduction of the beetles. This approximates the soil temperature up to a depth of 1 m, measured in the field at the beginning of March, following the severe winter of 1978/79. This temperature was, therefore, near the lowest the beetles may encounter underground in the field in The Netherlands. Even so the beetles progressed fairly rapidly (fig. 10). In a total of 60 cages filled with less densely packed sand (not exceeding 1.55 g/cm<sup>3</sup>) and at temperatures of 5–17 °C the shaft was excavated within 1–3 days.

The morphology of the shaft was very variable. However, a horizontal part was invariably present within a depth of 30 cm. During the process of excavation the female often made another horizontal or slightly sloping gallery where she left the sand plug while continuing deeper. The shaft terminated in an oblique or horizontal gallery 6–15 cm long: the future first brood chamber (fig. 9). The depth of the shaft varied considerably, as can be seen from table 3.

The diameter of the shaft is determined by the size of the larger of the two beetles. In the field, casts of twelve shafts were made using liquid paraffin wax that solidified on cooling, enabling the diameter of the shafts to be measured. The mean diameters of all shafts were then averaged: the overall mean was 14.2 ± 0.7 mm (S.E.).

#### Oviposition and behaviour prior to and following it

As soon as the female has terminated the burrowing she begins to make a small cavity (diameter about 0.5 cm) for the future egg by moving her head and fore legs in the blind end

of the almost horizontal terminal part of the burrow, alternately scraping some sand away and pushing part of it back. When she has finished she walks up and down the passage until the male arrives. The male joins the female, sometimes before she has finished the egg chamber, when he no longer encounters a sand plug to transport upwards. Then the beetles usually mate, as described before.

Copulation at this stage, i.e. prior to oviposition, is not obligatory but it is seldom omitted. After copulation the male starts scraping sand over a distance of about 10–15 cm from the bottom of the future first brood chamber. He may do this several times, so that a sand plug is formed. Then he turns around and transports the plug upwards. The female continues to prepare the egg chamber, breaking off to walk through the future brood chamber, with her abdomen pulsating. These pulsating movements are probably connected with the transport of an egg into the oviduct. Finally she moves her abdomen into the egg room and oviposits, making gentle pumping movements. Oviposition may last 10–25 minutes. After oviposition the female shows the backward scraping behaviour, just like the male, over a distance of some 10–15 cm, but in the opposite direction. Then she turns around and pushes the sand into the end of the burrow, thus sealing the egg chamber. The wall that thus separates the egg chamber from the future brood chamber becomes 10–15 mm thick (compare fig. 9). As a consequence of the scraping of sand by male and female the diameter of the brood chamber is slightly larger than that of the rest of the burrow: 15.0 ± 0.7 mm (S.E.), n = 12.

While the female is completing the egg chamber and preparing the brood chamber, the male is involved in widening the shallow horizontal part of the burrow, which is to become a store room for dung pellets. The diameter of the store room becomes 2–4 cm.

Table 3. Depth of shaft in *Typhaeus typhoeus* under laboratory and field conditions. [Temperature in the lab 5° or 9 °C; bulk density in glass cages and casks about 1.55 g/cm<sup>3</sup> to match field conditions. Enclosures 1 × 1 m<sup>2</sup>; casks 0.5 × 0.5 × 1 m<sup>3</sup>. Ample supplies of dung were provided in all experiments.]

year	experimental set-up	n	depth (cm)	range (cm)
1979	glass cages	lab	(2-dim.)	12    67 ± 22    29–100
1979	enclosures	field	(3-dim.)	5    69 ± 6    63–80
1980	glass cages	field	(2-dim.)	5    68 ± 9    52–78
1980	casks	lab	(3-dim.)	4    58 ± 13    46–78

### Dung provisioning

When she has finished preparing the brood chamber the female walks up the burrow to meet the male in the store room or, alternatively, if he is ready first, the male walks down after enlarging the store room. When they meet, the female pushes the male upwards firmly and vigorously sweeps his elytra with her fore legs. This continues, until the male finally makes for the surface to fetch dung, the female waiting for him in the store room or in the brood chamber.

When he has found a fecal pellet, the male usually takes it between his front tibiae and walks backwards with it to the nest entrance. Sometimes he holds the pellet between his mandibles, but I have never observed the pellet being carried on the horns as described by Fabre ( $\pm$  1910). The male drags the dung pellet into the direction of the nest entrance in a straight line, however tortuous his searching path may have been. If the dung pellet is found within about 40 cm from the nest entrance the male usually enters the hole at once. If the fecal pellet is found further away, however, the beetle drops it within 5—10 cm from the entrance and then moves directly to the entrance, walking forwards, puts his head into the entrance for a few seconds, turns around, picks up the dung pellet and carries it down without further delay. Whenever the beetle misses the entrance he finds it after an area-restricted search. This behaviour of searching for the entrance in the vicinity of the nest shows that the beetle is capable of roughly estimating the distance from the place where the dung was found. During the procedure of dragging a dung pellet from a fair distance away, the behaviour of leaving it behind and walking forwards to the nest entrance may occur more than once.

As soon as the male, dragging the dung pellet backwards into the nest, appears in front of the female below, she immediately begins to sweep his elytra. Then the male pushes the dung pellet underneath himself and walks up the shaft again to fetch more dung. The number of rabbit dung

pellets dragged in successively by the male does not usually exceed 30; it depends on the ease with which he can find them and the distance to be covered. The time needed to collect them also varies, but seldom exceeds two hours. After this bout of dragging dung pellets, the male stays below-ground for some hours.

The female takes a dung pellet from the store room and, holding it in her fore legs, lets herself fall down the shaft by drawing in her middle and hind legs close along the body. In the brood chamber she tears the pellet to pieces with the help of her mandibles and fore legs and then firmly presses the pieces into the blind end of the brood chamber with her head and thorax, intermittently turning around her length axis. This firm pressing causes a meniscate layering within the dung sausage that is going to fill the brood chamber. The female walks up the shaft to collect every dung pellet. Alternatively, the male may supply her with dung by carrying down a number of fecal pellets. Sometimes the male kicks the dung pellets out of the store room with his hind legs. As a consequence the lowest part of the burrow behind the female becomes filled with fecal pellets.

Often, the male walks down the shaft to the female. If the female progresses too slowly he may stimulate her and he often tries to copulate. When the female goes up to fetch more dung to provision the brood chamber and encounters the male before she reaches one of the pellets in the store room, she invariably stimulates him by sweeping his elytra. It thus appears that the co-operation of male and female in the stage of dung provisioning is often reset by interaction.

The number of rabbit dung pellets processed per dung sausage varies between 30 and 65, averaging about 40. The number of dung sausages manufactured varies between 4 and 21, averaging about 10 (table 4).

### Sealing the dung sausage and excavating the next brood chamber

When the dung sausage is finished the female

Table 4. Number of eggs laid (= dung sausages manufactured) in *Typhaeus typhoeus* under laboratory and field conditions. [Experimental conditions as mentioned in table 3.]

year	experimental set-up		n	number	range
1979	glass cages	lab	(2-dim.)	11	9.9 $\pm$ 4.3
1979	enclosures	field	(3-dim.)	5	10.6 $\pm$ 4.9
1980	glass cages	field	(2-dim.)	5	7.8 $\pm$ 2.9
1980	casks	lab	(3-dim.)	4	10.5 $\pm$ 1.7
					5—21
					6—19
					4—12
					8—12

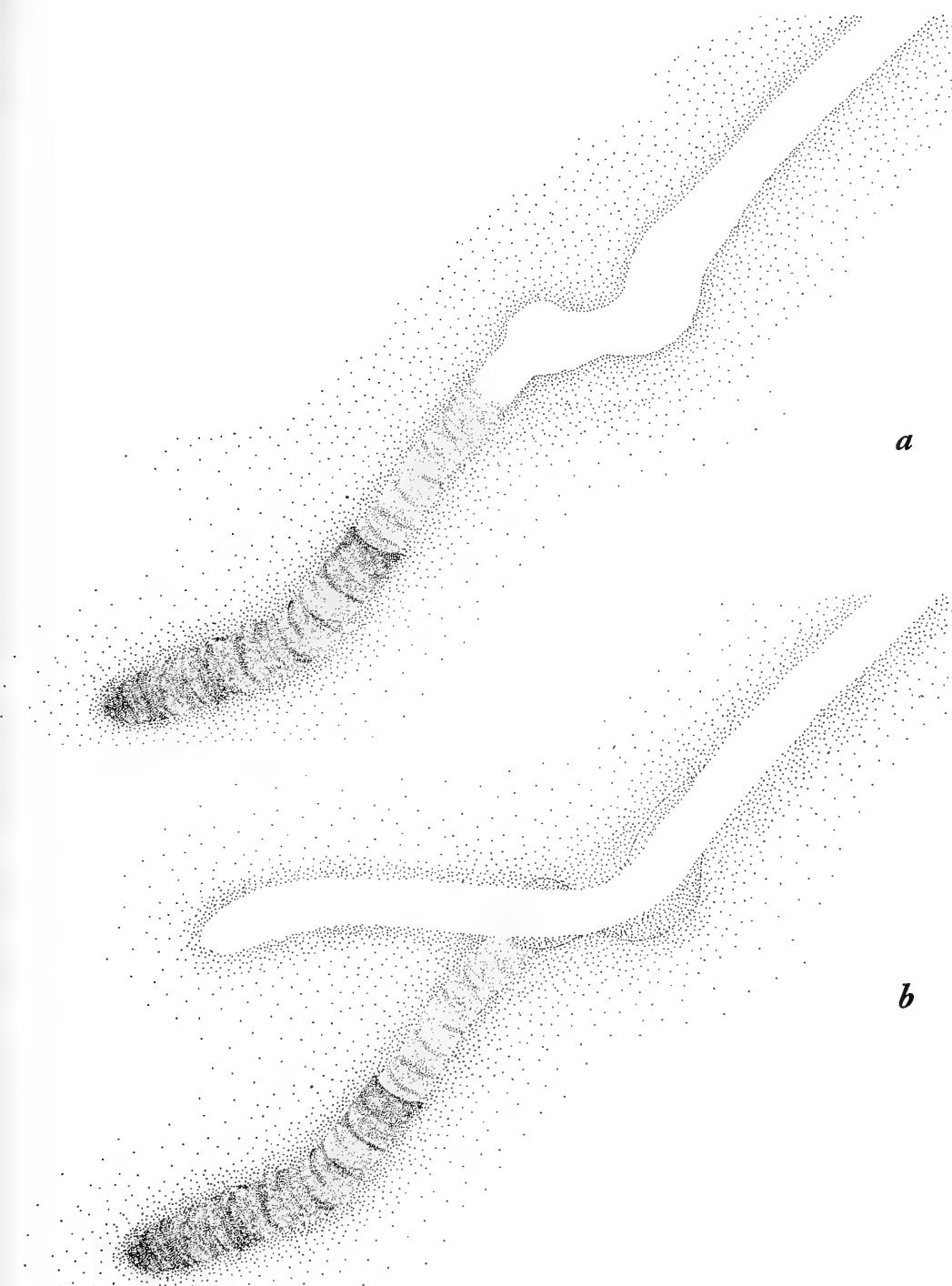


Fig. 11a. Dung sausage being sealed over a predetermined stretch with sand from the shaft walls. Fig. 11b. The widening is plastered with sand from the new brood chamber.

seals it with soil, using sand scraped from the wall of the shaft. Interestingly, this wall-scraping starts some cm above the proximal end of the dung sausage and in this way the amount of the shaft to be filled with sand is determined (fig. 11a). Only half way or later in the stage of sealing is the next brood chamber excavated. The widened part of the shaft above the sand plug that seals the former dung sausage is inadvertently plastered by the beetle with sand that it drops as it is carrying it upwards (fig. 11b). The next brood chamber is excavated above the former one (fig. 12).

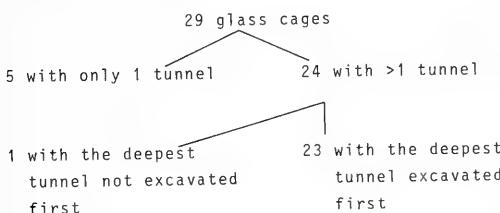


Fig. 12. Brood chambers are excavated above each other, beginning with the deepest.

Fig. 15 shows that the first tunnel excavated is usually the deepest. A tunnel is that part of the burrow from which one or more brood chambers branch off. This may be equivalent to a shaft, but more than one tunnel may be found branching off from the same shaft (fig. 9). A new tunnel is usually branched off when the latest brood chamber is relatively shallow. In the present study, the uppermost dung sausage in 22 cases with more than one tunnel was, on average, about 40 cm deep (table 5). While excavating the subsequent brood chambers the same behavioural sequence of transporting sand, copulation, oviposition and dung provisioning is shown.

As long as the male is present the female always excavates a new brood chamber, at times preceded by a new tunnel, irrespective of the availability of dung or the number of eggs already laid. If the male is no longer there, the be-

haviour of the female varies. If there is still a supply of dung she may continue the whole process of excavating a brood chamber, egg-laying, gathering dung and manufacturing dung sausages on her own. She may even excavate the next brood chamber with no male present and no dung around. If she has laid the next egg although there is no supply of dung, she may fill the newly excavated brood chamber with sand from the walls of the burrow, which shows that the behaviour after oviposition is fixed upon provisioning with whatever material there is around. Alternatively, the female may abandon the nest, invariably after finishing and sealing the last dung sausage, and continue reproduction elsewhere.

#### Behaviour of larvae and newly hatched adults

As soon as the egg has hatched the larva makes its way through the 1–1.5 cm thick sand wall that separates it from the dung sausage and moves into the dung in a somersaulting motion by which it displaces material from in front of it to behind it. As a consequence, after the larva has passed through, a small wad of dung, several mm long and wide, remains at the distal end of the dung sausage. The larva eats its way through the dung sausage, back-filling the space behind it with its excrement (fig. 13), so that the cavity surrounding the larva becomes only 2–3 cm long. It may eat its way through the dung sausage several times. There are three larval stages. Finally the larva III moves out of the dung sausage at the distal end and makes a cavity at the site of the former egg chamber: the pupal chamber. As a consequence, the distal end of the dung sausage becomes filled with sand displaced by the larva. The pupal chamber is plastered with excrement by the larva, which finally lies on its back to pupate (fig. 14).

After pupation the newly hatched adult often remains days or weeks in the pupal chamber before going to the surface. In my rearing trials, 45 out of 51 emerged adults passed through the partly eaten dung sausage, which thus appeared to be the rule. The other 6 immediately bur-

Table 5. Depth of uppermost dung sausage in shafts with more than one tunnel.  
[Experimental conditions as mentioned in table 3.]

year	experimental set-up	n	depth (cm)	range (cm)		
1979	glass cages	lab	(2-dim.)	10	36 ± 10	20 — 48
1979	enclosures	field	(3-dim.)	5	42 ± 12	35 — 54
1980	glass cages	field	(2-dim.)	3	38 ± 10	25 — 50
1980	casks	lab	(3-dim.)	4	32 ± 8	20.5—40.5



Fig. 13. Larva of *Typhaeus typhoeus* eating its way from the distal end (right) to the proximal end (left) of a dung sausage and back-filling it with its own excrement. (Photo of dung sausage and larva in glass cage.)

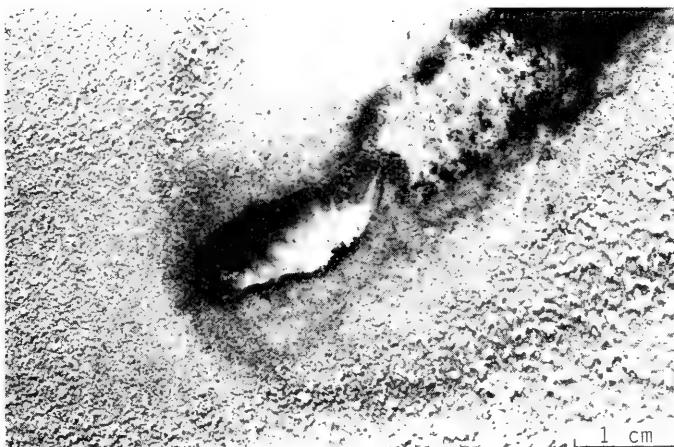


Fig. 14. Pupa of *Typhaeus typhoeus* in pupal chamber made outside the distal end of the dung sausage. The horn (right upper part of pupa) shows that this specimen will become a male. (Photo of pupa in glass cage.)

rowed their own way upwards from the pupal chamber. At least 23 out of the 45 passing through the old dung sausage subsequently also burrowed their own way upwards. I believe this to be the normal behaviour because after passing through the old dung sausage, the remaining

22 broke through the sealing sand and subsequently followed the old shaft, but they were most probably forced to do so by the cages, so this should be regarded as abnormal behaviour (see the arrows in fig. 9).

A beetle burrowing its way upwards scrapes.

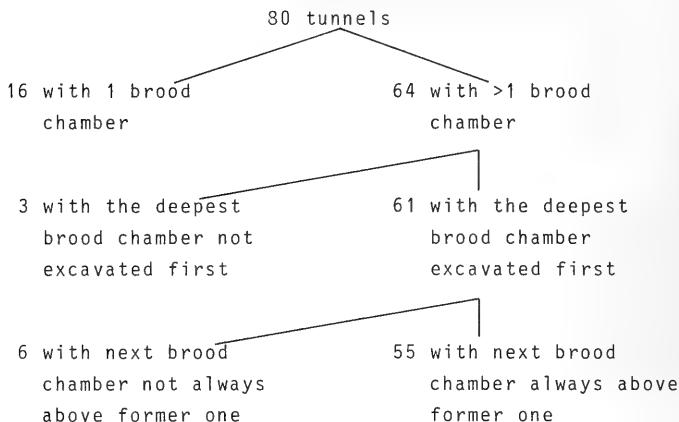


Fig. 15. The tunnel excavated first is usually the deepest.

the sand away above itself, turns around and firmly presses it behind. Consequently, at the beginning of this behaviour the space in the old dung sausage or in the pupal chamber is filled with sand. Subsequently, a corridor about 8 cm long steadily extends upwards through the soil, the beetle scraping sand away above and pressing it beneath itself. An emerging beetle reaches the surface within a few hours, depending on the depth from which it starts. On arrival at the surface the animal shows the behaviour as described in the section on emergence and maturation feeding.

## DEVELOPMENT

### Development of eggs and larvae

To study the (rate of) development of the different stages of *T. typhoeus*, beetles were reared in cages as described in the section on methods. The results of the rearing trials, which lasted almost three years, are given in tables 6 & 7, which cover the rearing period from winter 1979 to autumn 1980 and from autumn 1980 to autumn 1981, respectively. In the rearing trials the effect of administering cold winter periods was most noticeable. These cold periods were administered because soil temperature had been found to drop from 13 °C in August to 3 °C in February at a depth of 1 m in the field. At 0.20 m from the surface the fall in temperature was greater (from 16° to 1 °C).

After presenting the results of the rearing trials in the laboratory, the development of larvae in the field will be described. To facilitate com-

prehension, the course of development is briefly outlined in fig. 16.

### Rearing trials (1979—1980)

The rearing trials were carried out in rooms with constant temperatures of 1°, 5°, 9°, 13° and 17 °C, respectively. These temperatures were chosen because soil temperatures measured in 1979 in the study plot at Wijster (where *T. typhoeus* occurs naturally) ranged from 3—10 °C in the reproductive period and increased to 13—16 °C during summer, when the larvae develop. At all the temperatures they were subjected to, the beetles showed their reproductive behaviour.

At 1 °C only very few eggs were laid, however, and the dung sausages were abnormal, consisting partly or completely of whole dung pellets. The eggs did not hatch. Therefore the rearing trials carried out at 1 °C will not be discussed further. At 5 °C reproductive behaviour was normal, but the eggs did not hatch either, not even after 20 months. At a temperature at or exceeding 9 °C the eggs did hatch. The time eggs laid at 5 °C took to hatch at 9°, 13°, 17° and 20 °C was estimated (table 8). Though the number of observations is small in some groups (because this trial was not solely intended to study the hatching time of the eggs) it is quite clear that at 9 °C development is relatively slow. At the start of the rearing trials there were four cages at each temperature. However, three of the cages kept at 9 °C soon had to be discarded because in one cage the female died without reproducing and although

Table 6. Results of rearing pairs of *Typhaeus typhoeus* in glass cages at four different temperatures.

LARVAE		ADULTS		( P R E ) PUPAE		ADULTS	
number of weeks that elapsed from cold winter period until median number of beetles had emerged		number of weeks that elapsed from start of rearing trial until median number of beetles had emerged		first date with median number of beetles emerged		first date with median number of pupal chambers was present	
number of beetles that emerged		number of weeks that elapsed from cold winter period until median number of pupal chambers was present		number of weeks that elapsed from start of rearing trial until median chambers was present		first date with median number of pupal chambers present	
number of pupal chambers		number of larvae observed		number of weeks elapsed from start of rearing trial until median number of eggs was present		first date with median number of eggs present	
number of sausages = number of eggs		number of beetles of pairs		date of start of rearing trial		date of start of rearing trial	
temperature (°C)		rearing temperature (°C)		13°	28/29/111 1979	28/29/111 1979	13°
9°	28/29/111 1979	28/29/111 1979	9°	13°	28/29/111 1979	28/29/111 1979	17°
9°	21/22/1 1980	21/22/1 1980	9°	13°	28/29/111 1979	28/29/111 1979	17°
5	28/29/111 1979	4	4	5	2	22	2
9°	28/29/111 1979	21	21	13°	2	21	2
9°	21/22/1 1980	1	13	13°	1	1	1
13°	28/29/111 1979	4	4	13°	2	22	2
13°	28/29/111 1979	20	20	13°	2	21	2
13°	28/29/111 1979	17	17	13°	1	1	1
17°	28/29/111 1979	4	4	17°	1	1	1
13°	28/29/111 1979	4	4	13°	2	22	2
13°	28/29/111 1979	18	18	13°	1	1	1
13°	28/29/111 1979	17	17	13°	1	1	1
17°	28/29/111 1979	4	4	17°	1	1	1
13°	28/29/111 1979	5	5	13°	5	17 IV 1980	5
13°	28/29/111 1979	16	16	13°	6	17 IV 1980	6
13°	28/29/111 1979	14	14	13°	1	1	1
17°	28/29/111 1979	17	17	17°	1	1	1
13°	28/29/111 1979	55	55	13°	3	1	1
13°	28/29/111 1979	36	36	13°	6	1	1
13°	28/29/111 1979	52	52	13°	0	0	0
17°	28/29/111 1979	55	55	17°	6	1	1
13°	28/29/111 1979	78	78	13°	78	78	78
13°	28/29/111 1979	80	80	13°	80	80	80
13°	28/29/111 1979	76	76	13°	76	76	76
17°	28/29/111 1979	24	24	17°	24	24	24

- <sup>1)</sup> Stopped in November 1980, i.e. 20 months after the start.
  - <sup>2)</sup> Initially 4 pairs of beetles, soon declining to 1 pair, see text.
  - <sup>3)</sup> Artificial winter period at 5 °C from 5 XI 1980 to 23 I 1981.
  - <sup>4)</sup> Stopped in September 1981, i.e. 20 months after the start.

Data from pairs subjected to a cold period from 30 October 1979 to 28 February 1980 are presented on the right side of the relevant columns; data from pairs not subjected to a cold spell are given on the left side. Totals at the bottom of the table pertain to data from rearing trials at 13° C only (see text), hence the break in the table between the 9° and 13° C rows. There was a significant difference between the number of beetles that emerged from the cages receiving a cold treatment and those that emerged from the cages that did not receive a cold treatment:  $\chi^2 = 21.85^{***}$ .

Table 7. Results of ongoing rearing trials in glass cages from November 1980 until October 1981 in rooms kept at a temperature of 13° or 17 °C.

winter periods offered at 5°C as indicated in Fig. 12	number of pairs of beetles	5 November chambers	numbers on 1 July 1981	number of pupal emerged	numbers on beetles in 1981	number of pupating beetles not pupating	larvae remaining in larval chamber	a cold period and cold cages not given that treatment given	number of beetles emerged from number of cages that emerged	difference of beetles emerging females in sex ratio of emerging beetles (females : males)
- +	7	27	27	23	0					
+ +	7	2	+4 = 6	5	0					$\chi^2 = 20.12^{***}$
+ -	6	6	+1 = 7	0	2					(P << 0.005)
- -	7	11	+3 = 14	5	8					18 : 15

five dung sausages were made in each of the other two cages they were very superficial and the larvae soon died, probably because the fluctuations in moisture were too great.

On 30 October 1979, by which time virtually all the larvae had emerged, the cages were divided into two groups, one group remaining at the temperature it had been subjected to so far, the second group receiving a five-month cold spell at 5 °C until 28 February 1980, after which the cages were once again subjected to their former temperatures. The single cage remaining at 9 °C was assigned by chance not to receive a cold spell. One year later, rearing at 9 °C was repeated with one cage that was given a cold period (see table 6). The number of pupal chambers and the time that elapsed until they appeared can be read from table 6. At 9 °C the median number of pupal chambers was reached much later in the cage without a cold period than in the cages at 13 °C and 17 °C, whether or not the latter received the five-month cold spell. This

again indicates that development is very slow at 9 °C.

At 13 °C and 17 °C pupal chambers were made by the larvae of all groups. This proves that a cold period is not a prerequisite for making a pupal chamber. At 13 °C and 17 °C, in the groups receiving a cold period, the median number of pupal chambers was achieved after a similar period from the start of the trials: 55 and 52 weeks, respectively. The date by which half the beetles had emerged was also very similar for these two groups. Therefore, I felt justified in combining the data on the different stages in the cages kept at 13 °C and 17 °C (bottom of table 6). This resulted in a very significant difference between the proportions of beetles emerging from cages which had and those emerging from cages which had not been subjected to a cold period: only one beetle emerged from 19 pupal chambers in the latter, compared with twelve beetles out of 14 pupal chambers in the former ( $\chi^2 = 21.85^{***}$ ,  $P << 0.005$ ). Thus a

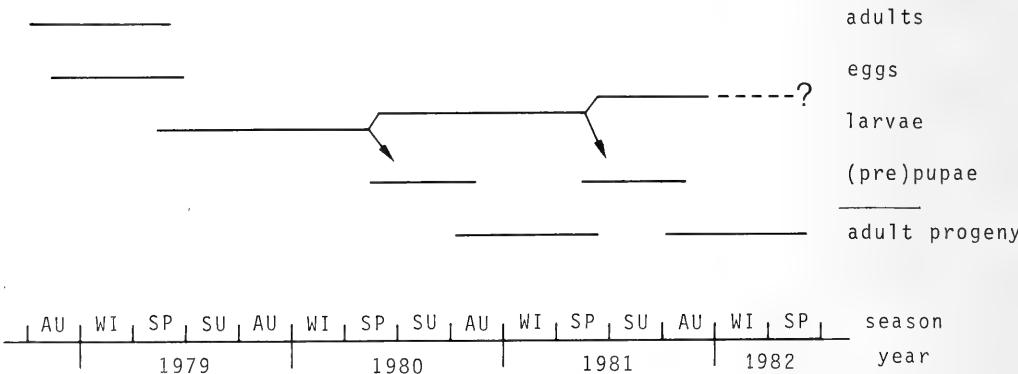


Fig. 16. Outline of development of life stages in *Typhaeus typhoeus*. At the bifurcations arrows indicate larvae changing into the pupal stage, while the continuous line indicates remaining in the larval stage.

Table 8. Numbers of eggs hatching and median time that elapsed before hatching in a rearing trial in glass tubes.

temperature (°C)	start dung on 28 August	number of tubes with egg and sausage at start	number of glasses	number of eggs that hatched	median number of eggs had hatched	number of weeks that elapsed until hatching
						1980
9°		5		3	7 - 8	
13°		44		39	3½	
17°		5		3	2½-3	
20°		5		3	2 - 2½	

cold period, although not a prerequisite, certainly favours the completion of the life cycle. The single beetle that emerged from a cage without a cold spell appeared in the same period as those from the cages subjected to a cold interlude (table 6).

Of the 13 beetles that emerged, six were females and seven were males: a 1 : 1 sex ratio.

From these results it can be inferred that soil temperatures in the field ranging from 3—10 °C in early spring to 13—16 °C in summer, favour reproduction and the development of the larvae.

Two other experiments in cages were carried out in early spring 1979, one at 5 °C and one at 9 °C. These will be reported in another paper. In June 1979, when reproduction in these experiments was over, the cages were taken to rooms in which constant temperatures of 13 °C or 17 °C, respectively, were maintained. Thenceforth these cages were exposed to the same treatments as those in the above-mentioned rearing trials, including the division into groups that did or did not receive the cold period. Data on pupal chambers and the beetles that

emerged are given in table 9. The results clearly confirm the conclusions already reached regarding sex ratio and effect of a cold spell on rearing results.

#### Rearing trials continued (1980—1981)

As mentioned before, in cages at 5 °C, the eggs had not hatched after 20 months. The two cages at 9 °C, one of which had received a cold winter period, were kept at 9 °C until 20 months had elapsed from the start of the rearing trials. By that time they contained three and one live larvae in pupal chambers, respectively. It may thus be surmised that even at such a low temperature adult beetles might have emerged after a (new) cold period.

Since the results of the 13 °C and 17 °C treatments of the three trials were similar and, moreover, the beetles emerged in the same period (tables 6 & 9), those cages that apparently still contained life after the period of emergence of the beetles, were pooled and subsequently divided into four groups for continued rearing. Two of the groups were subjected to a cold period at 5 °C from 5 November 1980 to 23 January 1981. This was done in such a way that after the rearing trials were completed all four combinations of 0 to 2 cold periods had been realized, as outlined in fig. 17. The results are given in table 7.

A beetle emerged from almost all pupal chambers in cages subjected to a cold period for the first time (23 beetles out of 27 pupal chambers). In cages that had already received a cold period during the 1979—1980 part of the rearing trials, only two pupal chambers remained in which the larva had not pupated. During the 1980—1981 part of the rearing trials this small number rose to six and, when subjected to a second cold period, a beetle emerged from five of

Table 9. Rearing results from two additional experiments. Data on left of columns pertain to glass cages that had not received a cold period. Data on right of columns pertain to glass cages that did receive a cold period.

pupal chambers	number of beetles emerged	number of beetles that emerged	median number of beetles	first date with receiving a cold winter period	number of beetles from glass cages not receiving a cold winter period	difference in number of beetles emerged (females : males)	sex ratio of emerging beetles
additional experiment (13°C)	15	0	-	30 IX 1980	{	$\chi^2 = 42.00^{***}$ (P << 0.005)	14 : 13
additional experiment (17°C)	8	2	27	25 IX 1980	{	$\chi^2 = 10.43^{***}$ (P < 0.005)	5 : 6

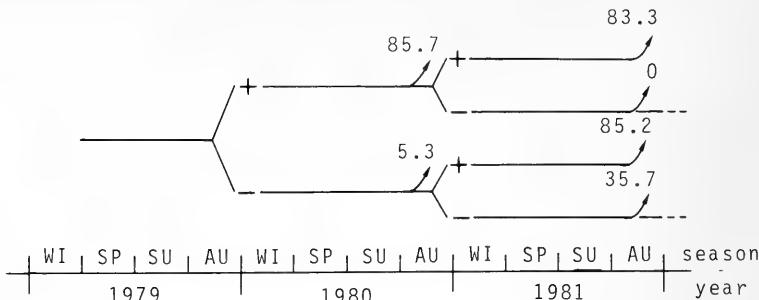


Fig. 17. Cold spell at 5 °C (+) or no cold spell (-; constant temperature of 13 °C or 17 °C) administered in rearing trials during 1979—1981 and percentages of adults emerging. Percentages pertain to numbers mentioned in Table 6, columns 8 and 12, and Table 7, columns 4 and 5.

these six pupal chambers. But in the cages not subjected to a second cold period no beetles emerged from the seven pupal chambers. Few beetles emerged from cages that received no cold treatments (five beetles from 14 pupal chambers). As in 1979—1980, the number of beetles that emerged after a cold period during the 1980—1981 part of the rearing trials differed very significantly from the number that emerged from cages not subjected to a cold period ( $\chi^2 = 20.12^{***}$ ,  $P << 0.005$ ).

Of the 33 beetles emerging from the cages in 1981, 18 were males and 15 females, which confirms the 1 : 1 sex ratio found the previous year. All twelve larvae remaining after the 1980—1981 part of the rearing trials were in their third instar (head capsules 4.6—5.2 mm).

#### Development of larvae in the field

Evidently, the quantity of cold that larvae of a given generation experience in the field during winter will differ because of the differing depths at which eggs are laid in the soil and because some winters are more severe than others. In general, the larvae occurring closest to the surface will experience more cold in winter and more heat in summer, which may accelerate their development vis-à-vis that of deeper larvae. To test this, five cages were dug into the soil in the study plot at Wijster in November 1979, in such a way that their upper edges just reached the surface.

At the beginning of March 1980 a pair of dung beetles and ample dung were introduced into each cage. The beetles were prevented from exchanging with the surrounding field population by wire-netting placed over the cages' walking surface. The cages were dug out at the

beginning of September 1981, by which time larvae that had completed their life cycle could be found as newly hatched but not yet emerged beetles; in addition, this was also the right time to check whether, as expected, some of the larvae had not yet completed their life cycle. The five cages proved to contain 39 dung sausages. In eleven of these a living larva was found, one of which was in a pupal chamber. All larvae were in the third instar (head capsules 4.5—5.0 mm). In addition, one newly hatched beetle was found. Though this is minimal evidence, the trial does demonstrate that under field conditions larvae of the same generation may give rise to adult beetles in different years, assuming, of course, that some of the remaining larvae would complete their life cycle in the future, as occurred in the laboratory rearing trials. Interestingly, the cage with the adult beetle also contained a larva in the pupal chamber and some other larvae, still in dung, which shows that different rates of development may occur in the offspring of one pair of beetles.

The results of another field trial, executed in the same period, enable a judgement to be made about whether the poor survival obtained in the above-mentioned field trial (life in 12 out of 39 cases = 31%) was somehow induced by the glass cages. In this trial five pairs of beetles were released in enclosures measuring  $2 \times 2 \text{ m}^2$ , at the beginning of March 1980. Their nests were dug up in May and June 1981, i.e. about three months earlier than the cages. There proved to be 32 dung sausages, 14 of which (i.e. 44%) contained a living larva; three of them had already made a pupal chamber. Assuming some mortality in the enclosures between May/June and September, the data suggest that there was

no difference in survival between the enclosures and the cages. Thus there is no evidence that the cages have a detrimental effect on survival.

#### Conclusions on rearing

The results from the rearing trials imply that the development of the larvae is very slow at 9 °C as compared with that at 13° and 17 °C. The latter temperatures closely approximate those in soil during summer. Some larvae pass through the life cycle at constant high temperature (17 °C). But the proportion of larvae that develop into adults is greatly improved by a cold period in the third larval stage. This condition matches to a varying degree the low soil temperature during winter. Depending on the experience of a cold winter period, larvae of the same generation and even from the same pair of beetles may give rise to adults in different years. So the life cycle may last three instead of two years and perhaps even longer. This variation in the duration of the life cycle enables genetic exchange between reproductive pools to be passively achieved in successive years.

#### Longevity of adults

Genetic exchange between reproductive pools in successive years might also be achieved if adult beetles reproduced more than once. This is unlikely to be the case in *T. typhoeus*, since in all laboratory trials executed at a temperature above 5 °C and in all the field trials, the beetles died shortly after reproduction. In many insect species, the dissection of females starting repeated reproduction reveals the presence of yellow bodies ( *corpora lutea*) at the terminal ends of the ovarioles; these are the remnants of the follicular epithelium, which degenerates after egg release (Krehan, 1970; Vlijm & Van Dijk, 1967). To investigate whether yellow bodies are formed and can be found in *T. typhoeus*, adult females were collected in the course of their active period and subsequently dissected. Moreover, females from several experiments that died after reproduction were dissected. Of 14 females that died after reproduction, three proved to possess  *corpora lutea*. This indicates that in *T. typhoeus* yellow bodies are not always formed to an extent that they can be recognized. Of 52 females, captured in the field in the course of the season, eight possessed distinct  *corpora lutea* and three only a vague indication of these. These eight females were captured late in the season (May and June). Obviously, it was not known whether these females were on their

way to aestivate or to die.

Clearly, the absence of yellow bodies does not allow conclusions to be drawn about repeated reproduction, and only if their presence is established at the onset of the reproductive period can these bodies be used as indicators of repeated reproduction.

Therefore, an experimental approach was followed. A trial to have beetles aestivated and let them reproduce in the following activity period was executed twice. From May 1979 onwards, 60 beetles, captured when newly emerged in October and November 1978, were kept in plastic jars (13 cm deep, 10 cm in diameter; one beetle per jar) containing moist sand at a temperature equal to that measured in the study plot at Wijster 20 cm below the surface. Natural daylength was applied. The beetles were regularly supplied with fresh rabbit dung. Of the 60 beetles, 25 had survived after reproduction (13 males and 12 females) before May at a constant temperature of 5 °C. The other 35 (23 males and 12 females) had been kept at 5 °C in the jars since their capture. By 2 August 1979 all the beetles had died except for two males (one male from each group). Shortly thereafter the temperature-regulating equipment in the laboratory broke down and the beetles died from heat.

In 1980, 25 beetles that had not reproduced but that had been kept in plastic jars at 5 °C since their capture in autumn 1979 were used in a trial. No beetles that had already reproduced were available. In mid-March 1980 these 25 beetles were divided into four groups: staying at 5 °C (three males, one female); 9 °C (six males, three females); 13 °C (five males, one female); and 17 °C (five males, one female). By 1 July all the beetles kept at 9°, 13° and 17 °C had died; two males at 5 °C were still alive. These two males survived and were given the chance to pair with two fresh females in glass cages on 27/28 November 1980. One male died on 2 December without having reproduced, the other died on 15 December after the female had laid a few eggs.

From the results of the dissection and of the trials, it can be concluded that aestivation of adult beetles and repeated reproduction in *T. typhoeus* is very exceptional, if indeed it occurs. Most of the beetles die after the first reproductive season. Thus the contribution to genetic exchange between reproductive pools in successive years by means of survival of adults is virtually non-existent.

## DISCUSSION

### Influence of glass cages on behaviour and results of rearing

Although the behaviour of the beetles seemed normal, the narrow space in which they were confined may have influenced their behaviour. Tables 3 & 4 show that there were no major differences in the depth of the shaft and number of dung sausages between beetles kept in the laboratory and those kept or found in the field. Moreover, the number of dung sausages produced in the present trials was very comparable with figures reported in the literature (tables 2 & 4). As reported in the section on the development of eggs and larvae, the survival of larvae kept in glass cages dug into the soil and kept in enclosures in the field was similar. This confirms that glass cages do not adversely affect the behaviour of the beetles.

### Pheromones

There are few data on settlement and pair formation in the literature. Halffter & Matthews (1966), in their extensive review of the biology of Scarabaeidae, assume that the sexes meet by chance near the dung patch. In addition to the case of *Typhaeus biostius* mentioned earlier (Crovetti, 1971), the intrusion of a male into a female's feeding burrow and joint feeding until sexual maturity, is also reported by Rommel (1961) in *Copris hispanus* and by Halffter & Lopez (1977) in *Phanaeus daphnis*. The hypothesis of pheromone communication in *T. typhoeus*, tentatively suggested in the present paper, is supported by reports that in Scarabaeidae some dung patches are densely populated with beetles, whereas others are not, and that the densely populated dung patches often differ from each other in the taxon that is most represented (e.g. Halffter & Matthews, 1966; Paschalidis, 1974). A similar clustered distribution is known in bark beetles (Scolytidae), and this is known to be caused by aggregation pheromones (Blight et al., 1980). By analogy, pheromones may be important in dung beetles, too. Moreover, the stance adopted by the male *T. typhoeus* during the supposed pheromone release is virtually the same as that described by Paschalidis (1974) in three scarabaeid *Sisyphus* spp. and by Tribe (1975) in *Kheper nigroaeneus*. In the latter case pheromone release was proved. In *Kheper* the pheromone is released from a depression on either side of the first abdominal sternite, with the help of paraffin tubules as a

carrier. This is very different from the way the pheromone is supposed to be released by *T. typhoeus*, i.e. along with the excrement. The latter mechanism is also known for other groups, e.g. in bark beetles, boll weevils and some Orthoptera (Jacobson, 1972). If properly supported by additional research, pheromone release by *T. typhoeus* would constitute the first known example of pheromone communication in Geotrupidae. The conformity in releasing stance and the difference in releasing mechanism point to a convergent development and may be added to arguments in favour of the modern view of classifying scarabaeids and geotrupids in distinct families (Crowson, 1967, 1981) instead of in subfamilies (Halffter & Matthews, 1966).

In all cases the pheromone release stance has so far only been described in male dung beetles. The possibility should not be excluded, however, that after maturation feeding the male is also attracted to his first female by means of pheromones. Fabre ( $\pm$  1910) had already noticed that at times two or three males of *T. typhoeus* can be found in a burrow with only one female. Teichert (1955) observed the same in *G. mutator* and from this he inferred that males were attracted by pheromones released by the female. This would certainly improve the female's chances of mating. It has been stated by Halffter & Matthews (1966) that the similar size of the antennal clubs in almost all male and female dung beetle species is a sign of the unimportance of pheromone communication in these beetles. But this argument does not hold if both sexes respond to pheromones.

### Burrowing

One may wonder how much faster the female progresses in the burrowing stage thanks to help from the male. The gain is estimated by Teichert (1957) to be one-fourth to one-third of the excavation time.

Co-operation between male and female in the burrowing phase is not so close in some species as it is in *T. typhoeus*. It is marked in the relatively deep burrowing species *Geotrupes vernalis*, *Lethrus apterus* and *Typhaeus biostius*, whereas in the shallow burrowing species *G. mutator*, *G. stercorarius* and *G. spiniger* the male does little more than remove some soil from the entrance (Teichert, 1955, 1959a, 1959b; Crovetti, 1971).

According to Klempener (1979), in *G. spiniger* the female stops excavating the shaft and the brood chamber as a response to their length.

### Behaviour preceding and following oviposition

Oviposition in *T. typhoeus* is almost always preceded by copulation. According to Weaver & Pratt (1977) repeated copulation has a stimulating influence on the reproductive effort in the cockroach *Periplaneta americana*. This is probably why a female of *T. typhoeus* that has lost the male continues reproduction much more slowly.

During the backward scraping activity that follows oviposition, the beetle presses its head and thorax hard against the walls of the brood chamber, possibly to make the walls resist the pressure they will be subjected to when being provisioned with dung. Although he did not observe the pressing behaviour, Fabre ( $\pm$  1910) noticed that the walls of the brood chamber were smoother than those of the shaft.

### Dung provisioning

One may wonder how the male orients himself on the surface, when dragging a dung pellet to the nest entrance. Kuyten carried out some unpublished experiments in 1961/62 from which he concluded that the position of a light source provides the beetle with a directional cue. The same conclusion was independently reached by Frantsevich et al. (1977) after some very similar experiments with *Lethrus apterus*. But it has not yet been explained how *typhoeus* takes its bearings by night or on cloudy days, when most of the excursions for dung are made.

### Sealing and excavating brood chambers

Klemperer (1979) states that in *Geotrupes spiniger* sealing a dung sausage is a side-effect of excavating the next brood chamber. In *Typhaeus typhoeus*, however, at the start of sealing the sand is scraped from the wall and firmly pressed into the shaft above the dung sausage. Moreover, the last dung sausage is invariably sealed; this is also evidence of a distinct behavioural phase.

In the endemic Sardinian species *Typhaeus biostius*, which closely resembles *typhoeus* both in its biology and in the reproductive season, the sequence of excavation of brood chambers is remarkably different. Contrary to *typhoeus*, *biostius* constructs the uppermost dung sausage first, at about 60–70 cm below the surface, and every subsequent sausage is 10–15 cm deeper, the completed burrow generally reaching a depth of 1.30–1.60 m. As a result, under field conditions some weeks after the nest has been

completed the uppermost dung sausage already contains a larva III, whereas the egg belonging to the lowest dung sausage has not yet hatched (Crovetti, 1971). This behavioural sequence may well be related to soil moisture conditions (Crovetti, pers. comm., 1981), the female beginning to lay eggs approximately at ground-water level and then deeper as the water table falls. The ultimate function of this sequence may be to ensure that eggs and larvae do not dry out during the hot summer.

In *T. typhoeus*, however, the risk of drying out may be considerably lower. In this species, laying the first egg approximately at ground-water level and thenceforth more shallowly may ensure that the larvae and their dung sausages do not become waterlogged during the next winter. In this context it would be interesting to study the behavioural sequence in *typhoeus* in the southern part of its geographical range.

### Emergence through soil

The way the beetle moves to the surface is seldom mentioned in the literature. Sano (1915/16) reports that *Geotrupes stercorarius* does not always use the original tube made by the parents, but makes its own route, as described for *Typhaeus typhoeus* in this paper. Crovetti (1971) reports that *T. biostius* breaks through the partly eaten dung sausage and the sand that seals it and follows the shaft made by the parents. The evidence available for *T. typhoeus* (this paper) and for *T. biostius*, suggests that the newly hatched beetle starts moving upwards at a place where the resistance from soil is least, i.e. through the remnants of the dung sausage. However, it seems to be luck, rather than strategy, whenever the beetle finds the open part of the parental shaft. Emergence through soil thus seems to be the rule.

### Behaviour as a reaction chain

According to Klemperer (1979) the nesting behaviour of *Geotrupes spiniger* can be described as a reaction chain in which each action generates its own terminating stimulus and initiates the subsequent response. Although experimental analysis is beyond the scope of the present paper, the nesting behaviour of *T. typhoeus* is in many respects very similar to that of *G. spiniger*. In addition, the way in which the stretch of the burrow that is to be filled with sealing sand is determined in *T. typhoeus* (fig. 11) is an example of an action that generates its own terminating stimulus. So it may well

be that the behaviour of *typhoeus* can also be described as a reaction chain. The extent to which signalling between the sexes by means of pheromones, sweeping each other and stridulation alters this picture requires further research, however.

#### The role of temperature in diapause and development

Diapause is induced in the third larval instar and can be overcome by a cold winter period at 5 °C. Tauber & Tauber (1976) rightly point out that this does not prove that diapause develops under the influence of low temperature in nature, as in many instances diapause can artificially be broken in several ways, including manipulation of day-length and administering a high temperature. Yet it is difficult to imagine an environmental stimulus other than temperature that would induce, maintain and develop the diapause in larval dung beetles, since they live in complete darkness and in well-drained soils in which, over the year, differences in moisture are rather unpredictable. On the other hand, although temperature is known to be the single environmental stimulus maintaining rhythms in a number of insects during the day (Saunders, 1976), total reliance on temperature as a diapause-regulating factor in the course of the year has, to date, only been reported in tropical insects (Tauber & Tauber, 1976).

Regarding the role of temperature in larval development, the few larvae that deviated from the general pattern in the rearing trials (tables 6 & 7) are interesting. Some larvae did not complete their life cycle after a cold period. This suggests there may be considerable variation in the amount of cold (duration and/or degree) a larva needs before diapause is terminated. On the other hand, some larvae completed their life cycle without a cold interlude. As the latter were from the cages kept at 17 °C this suggests that a relatively high temperature can also overcome diapause. Raising the temperature from 15° to 21 °C has, for example, been shown to be sufficient to overcome diapause in rearing trials of *Geotrupes spiniger* (CSIRO, 1980: 66). This should be further studied in *T. typhoeus*, since it may mean that in the southern part of the geographical range a warm period in the first summer (summer 1979 in fig. 16) may be sufficient to enable the species to pass through its life cycle within one year. This may help to explain why Fabre ( $\pm$  1910), working in southern France, found a one-year life cycle in his first

rearing trial (though not in his second). The same phenomenon may occasionally occur in the northern part of the geographical range too, e.g. in a hot summer, but as a rule in those regions development will continue after a cold period in winter (winter 1980 in fig. 16), which thus leads to a life cycle of a minimum of two years. Spaney's suggestion (1910) (he worked in Germany) that in most cases *T. typhoeus* has a one-year life cycle, should be regarded with suspicion. Main (1916/17), working in England, found a two-year cycle. Though most Geotrupidae have a one-year life cycle, some are known to show a cycle of at least two years (Sano, 1915/16; Main, 1916/17; Howden, 1955).

Field results support the hypothesis that larvae of the same generation develop at different rates: the rearing trial in glass cages, dug into the soil and started in March 1980, yielded one adult beetle and a number of larvae in their final instar in the autumn of 1981 (see section Development, p. 224). But as only one adult beetle emerged, the hypothesis that the rate of development is related, by means of temperature, to the depth at which the larvae develop, could not be tested.

Regarding the development of eggs laid before the turn of the year, it is unlikely that these eggs can hatch before winter, let alone reach the third larval stage, since soil temperature at 20 cm to 100 cm below the surface is uniformly  $\pm$  9 °C by late October and subsequently decreases. As a consequence, the eggs do not hatch until early spring together with the eggs laid by that time, and the larvae do not experience a cold spell until the following winter. It may thus be inferred that a one-year life cycle probably cannot be achieved in The Netherlands, starting from these early eggs. This may not be true, however, in the southern part of the geographical range.

#### Flying

The Geotrupidae differ greatly in their use of flight. As early as 1910, Spaney remarked that *Geotrupes stercorosus* and *Typhaeus typhoeus* can rarely be observed flying, whereas *G. stercorarius* regularly flies. He thought this was because beetles of the first two species generally find plenty of food around in the place where they emerge and reproduce, whereas those of the last need to move from one fresh dung source to another. As regards the significance of the flying behaviour in the life history of *T. typhoeus*, three observations seem to be relevant.

First, the behaviour is shown in the laboratory in the presence of an ample supply of dung. Second, most of the beetles captured flying in the field did not have an empty gut. And third, I have observed the flying behaviour in the field in places with adequate supplies of dung that are apparently easily accessible to the beetles. This shows that flying is not solely connected with a shortage of dung and it may well be that flying is mainly related with searching for a partner. At the end of the season, however, there may be less dung available because it has been used by the beetles and because the density of the rabbit population has decreased, and then the beetles may fly in search of new dung supplies. This aspect needs to be studied further.

#### Persistence of populations in space and time

Clearly, much speculation remains about the cause and function of flying in adult *T. typhoeus*. There is also speculation about the selective forces that have led to and maintain the pronounced differences, both within and between pairs of reproducing beetles, in the depth at which the eggs are laid. Ignoring the causes, the different rates of development of larvae from one generation lead adult beetles to emerge in different years; this passively contributes to a reduction of the risk of local population extinction in time. Similarly the dispersal of adults results in, although is not necessarily aimed at, reducing the risk of local population extinction in space (Den Boer, 1968). The extent to which these phenomena contribute to the persistence of *T. typhoeus* populations within a certain area merits further study.

#### OUTLOOK

The present investigation of the biology of *Typhaeus typhoeus* will prove to be invaluable for the follow-up studies. Among the most important findings for the understanding of soil morphology and soil formation are: first, the observations of how, and to what extent, the burrows are excavated and, in particular, subsequently back-filled with dung and soil; and, second, the way in which newly hatched adult beetles make their way to the surface.

For the understanding of environmental factors (including soil conditions) that play a role in the species' burrowing behaviour and reproductive performance, results of rearing trials will prove indispensable.

Apart from these aspects, which are closely

related to the soil-oriented approach of the study, the present investigation reveals a number of starting points that may also be worth developing. The co-operation between male and female is so striking that further study is promising both from an ecological point of view (what is the gain in time and energy for the female and in net reproduction for both partners?) and, if carried out as a comparative study of related species, from an evolutionary point of view (how and when did co-operation develop?). In addition, the role of contests and the probable role of pheromones deserve further study, both in pair formation and in the exploitation of food resources. These aspects, pheromones and co-operation (and concomitant interaction) between the sexes, may reveal new insights in future ethological analyses of the nesting behaviour of dung beetles. Finally, a long-term study may reveal how much the differential development time of larvae and the dispersal of adults contribute to reducing the risk of local population extinction and to stabilizing beetle numbers.

Such studies may reveal the adaptive value of numerous aspects of dung beetle behaviour, about which we can only speculate at present.

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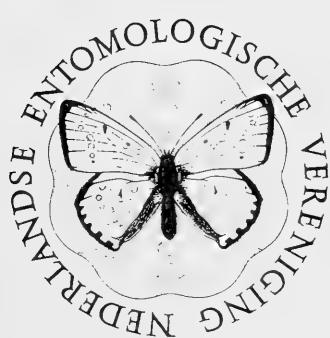
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R. DE JONG. — Annotated list of the Hesperiidae (Lepidoptera) of Surinam, with descriptions of new taxa, pp. 233—268, figs. 1—69.



# ANNOTATED LIST OF THE HESPERIIDAE (LEPIDOPTERA) OF SURINAM, WITH DESCRIPTIONS OF NEW TAXA

by

R. DE JONG

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## ABSTRACT

A list is given of all known species of Hesperiidae of Surinam, based on the literature and examined material. Material not yet recorded in the literature is listed with locality data. Notes are given on many species, and the following taxa are described as new: *Elbella bicuspis* (spec. nov.), *Urbanus ambiguus* (spec. nov.), *Bungalotis sipa* (spec. nov.), *Clito jonkersi* (spec. nov.), *Cymaenes geijskesi* (spec. nov.), *Vehilius major* (spec. nov.), *Mnasitheus similis* (spec. nov.), *Cobalopsis dorpa* (spec. nov.), *Cobalopsis tanna* (spec. nov.), *Morys subgrisea paradoxa* (subspec. nov.), *Eutychide subpunctata intermedia* (subspec. nov.), *Phlebodes meesi* (spec. nov.), *Penicula criska extrema* (subspec. nov.), *Polites vibicoides* (spec. nov.), *Panoquina panoquinoides minima* (subspec. nov.), *Cravera rara* (gen. nov. and spec. nov.), *Surina unica* (gen. nov. and spec. nov.).

## INTRODUCTION

Surinam has been popular with lepidopterists and naturalists in general since the early days of nature exploration. The famous water colours of Surinam insects by Maria Sibylla Merian, who lived from 1647 until 1717, testify of this early interest, and the large number of Lepidoptera from Surinam described by Cramer (1775—1780, continued by Stoll, 1780—1791) speaks volumes. A general impression of entomological research in Surinam up to 1950 was given by Geijskes (1951). As far as Hesperiidae are concerned three works are important, viz., Cramer (just mentioned), Sepp (1829—1852, for publication dates, see De Jong, in press), and Möschler (1876, 1882). Cramer described 78 species of Hesperiidae from Surinam, Sepp 21 species, and Möschler listed 145 species. The work of Sepp is not outstanding because of the number of species described or the quality of the plates, but owing to the very detailed descriptions of the larvae, pupae and food plants, all described species having been bred.

Shortly before Sepp started the publication of the work on Surinam Lepidoptera, Collin's thesis on the fauna of Surinam was published (1822, see Holthuis, 1958). This rare work is of little importance, since as far as the butterflies are concerned it is a not very accurate compilation of the species mentioned by Fabricius (1793) from Surinam.

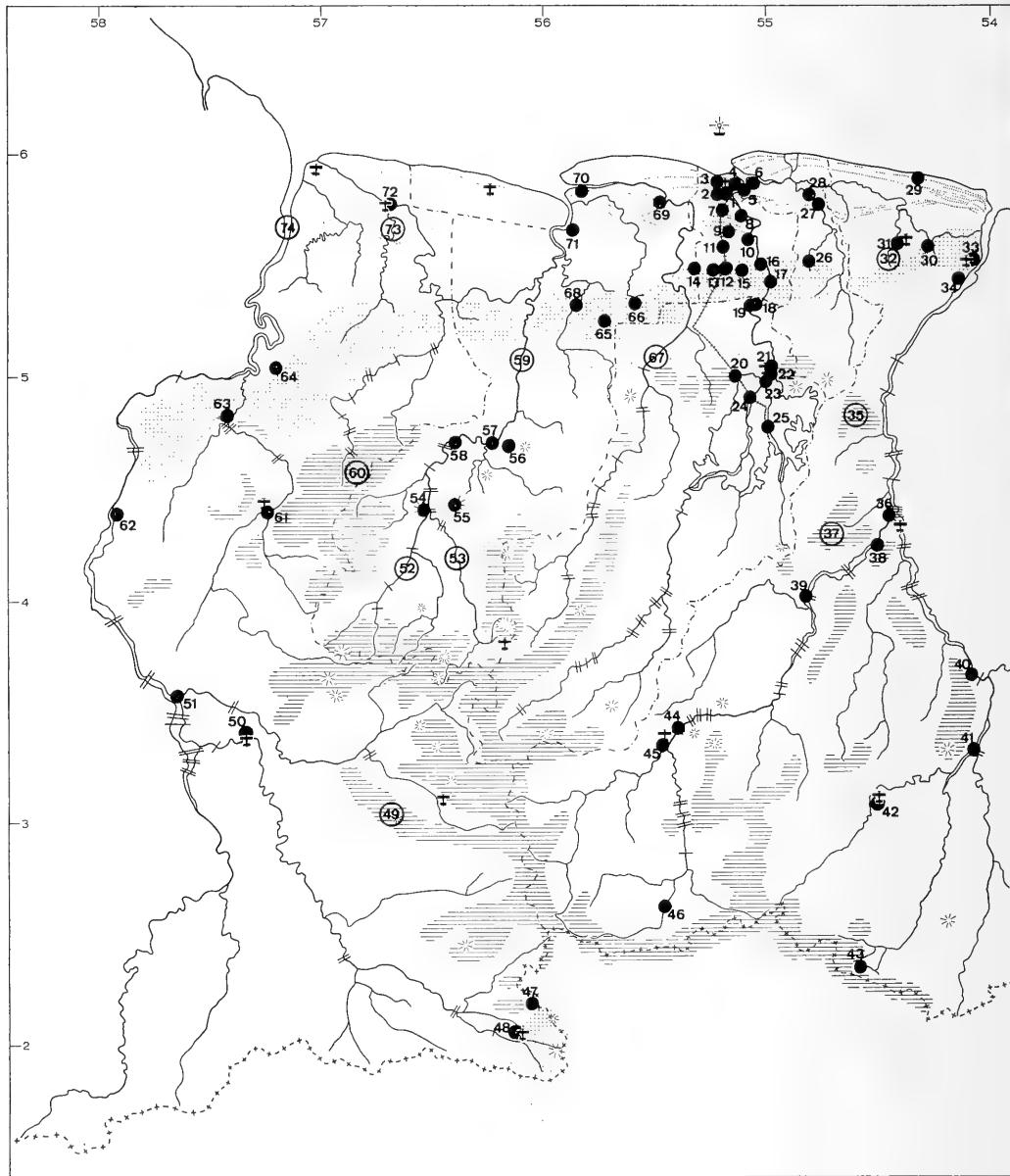
After Möschler, Surinam butterflies are only incidentally mentioned in the literature. In 1951, however, Evans (1951—1955) started the publication of the catalogue of all American Hesperiidae in the British Museum (Natural History), London. That museum proved to have 194 species from Surinam.

In the Netherlands the interest in South American Lepidoptera, already diminished in the beginning of the 19th century in a period of general impoverishment, seemed to have come to a standstill after the publication of Sepp's work, at least if judged from the complete lack of publications on Surinam butterflies up to the present time. The very limited edition of the latter work is significant in this respect. Although a scientific approach to entomology was gaining ground at the time in the Netherlands, most entomologists were interested in the Dutch fauna or the fauna of the Dutch East Indies. Nevertheless, limited amounts of material from Surinam were still sent to the Rijksmuseum van Natuurlijke Historie, Leiden, e.g. by W. C. van Heurn and the Penard brothers (1908), while the druggist Bolten, who lived in Paramaribo from 1902—1910, presented his small collection of insects to the museum. More important material was assembled much later. Dr. D. C. Geijskes, entomologist of the Agricultural Experiment Station at Paramaribo, later biologist at the Department of Home Affairs and Direc-

tor of the Surinam Museum at the same place, lived in Surinam from 1938—1965. He collected all kinds of insects during his expeditions into the interior all over the country. His material, now in the Rijksmuseum van Natuurlijke Historie, is not only important because of its quantity, but because of the outlying districts represented. As Geijskes, like most other collectors in Surinam, was not particularly interested in

Lepidoptera, the number of species in his material is limited, but as he also collected many small and dull-coloured species (also by running a Malaise trap) instead of restricting himself to the bigger and more brightly coloured ones as too often done, his material is quite interesting.

By far the best collection of Lepidoptera from Surinam was made by E. H. Jonkers, who lived in Surinam from 1956—1975. As an amateur-



naturalist he collected mainly Lepidoptera. His collection, which came to the Rijksmuseum van Natuurlijke Historie in 1977 and 1980, contained a large number of species, most being represented by rather few specimens. He mainly collected in the vicinity of Paramaribo, but also made many trips into the interior of Surinam. It is remarkable that some species represented in the smaller collection of Geijskes, are absent from the Jonkers collection, probably due to a different way of collecting.

Smaller amounts of Lepidoptera from Surinam are received irregularly by the Rijksmuseum van Natuurlijke Historie from biologists working in Surinam for a longer or shorter period. Among these I like to mention my colleague Dr. G. F. Mees, who visited Surinam several times as an ornithologist and found time to

make some interesting collections of Lepidoptera.

The total number of species of Hesperiidae known (or at least recorded) from Surinam now amounts to 426. Eight of these are, however, highly unlikely and probably due to false locality data or misidentifications. It seems to be a fair number, but as 126 species of Hesperiidae recorded from Guiana and/or French Guiana have not yet been found in Surinam, and the interior of the Guianas is still largely unexplored lepidopterologically, the total number of skipper occurring in Surinam must be far more than 500 and probably even exceeds 600. In spite of the apparent incompleteness of our knowledge of the Surinam Hesperiidae it seems worthwhile to publish a list of what is known at present, one hundred years after the last list

Fig. 1. Localities of Hesperiidae in Surinam. Black dots represent more or less exactly recorded localities; circles placed over mountains (hatched areas) or rivers indicate that the locality is not exactly known and could be anywhere in the mountains or along the rivers indicated.

Afobaka 22	Gransoela 39	Oele mari 42
Alalapadoe 47	Groningen 69	Onverdacht 9
Alamandidon 44		Palaomeu 46
Albina 33	Hebiwerie 54	Paramaribo 1
Avanavero Vallen 63	Jodensavanne 17	Paranam 10
Bakhuis Gebergte 60	Kabalebo 61	Parwabos 3
Batavia 71	Kabelstation 24	Patamakka Rivier 32
Belwaarde 5	Kabo 65	Pepejoe 45
Benzdorp 40	Kayser Gebergte 49	Phedra 19
Berlijn.13	Koffiekamp 23	Potribo 27
Bigiston 34	Kroetoe 55	Powakka 15
Blakawatra 16	Kwatta 2	Raleigh Vallen 57
Blauwgrond 4	Lawa 41	Rama 18
Boniface 1	Leiding 1	Rechter Coppename 53
Brokopondo 21	Lelydorp 7	Republiek 11
Brownsberg 20	Lely Gebergte 37	Sara Kreek 25
Caledonia 70	Leonsberg 4	Saramacca 67
Carolina Kreek 12	Linker Coppename 52	Sipaliwini 48
Charlesburg 1	Lucie Rivier 51	Stoelmans Eiland 36
Coeroeni Eiland 50	Makambi Kreek 24	Temomairem 43
Copi 26	Manlobbi 38	Tibiti 68
Coppename 59	Maratakka 73	Vier Kinderen 1
Corantijn Rivier 74	Ma Retraite 4	Voltzberg 56
Cultuurtuin 1	Mariënburg 6	
Domburg 8	Matapi 64	
Ephraïms Zegen 1	Matta 14	
Fallawatra Kreek 57	Moengotapoe 30	
Gansee 25	Moengo 31	
Goliath Kreek 66	Morico Kreek 28	
	Nassau Gebergte 35	Zanderij 12
		Zorg en Hoop 1

(Möschler, 1882). It does not seem likely that the number will increase largely in the near future. Moreover, several species are new to science, and publication may be a stimulus to further research.

In view of the incomplete knowledge of the species composition in Surinam and of the distribution of the recorded species in Surinam as well as in South America in general, no attempt has been made to analyse the species as to possible distributional types. At the moment the impression is, that by far most of the species recorded from Surinam have a wide distribution in tropical South America.

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#### LIST OF THE HESPERIIDAE OF SURINAM

In the list below I have followed the sequence and nomenclature adopted by Evans (1951—1955), unless recent literature or the material studied gave cause to deviation. The species name is followed by a reference to the literature records from Surinam if any (records by Evans always refer to the collection of the British Museum (Natural History), London), and the number and localities of specimens from Surinam in the following institutions: Instituut voor Taxonomische Zoölogie, Zoölogisch Museum, Amsterdam (abbreviated: ITZ); Nationale Zoologische Collectie, Universiteit van Suriname, Paramaribo (NZC); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); by far the most extensive collection of Surinam Hesperiidae).

(München (ZSM; all Surinam material originating from Fruhstorfer, no precise locality data). All localities are given on a map (fig. 1). Notes and descriptions of new taxa are given after the list.

#### Pyrrhopyginae

*Pyrrhopyge phidias* Linnaeus, 1758. — Evans (1951); Hewitson (1866); Williams & Bell (1931). RMNH: 6 ♂, 2 ♀, Brownsberg, Paramaribo, Surinam, Vier Kinderen. ZSM: 3 ♂, 1 ♀, Surinam. See Note 1.

*Pyrrhopyge aziza lexos* Evans, 1951. — RMNH: 3 ♂, Brownsberg.

*Pyrrhopyge proculus cintra* Evans, 1951. — Evans (1951). RMNH: 2 ♂, 2 ♀, Domburg, Lely Gebergte, Patamakka Rivier, Surinam. ZSM: 1 ♂, 1 ♀, Surinam.

*Pyrrhopyge thericles ponicea* Evans, 1951. — Evans (1951). RMNH: 2 ♂, 1 ♀, Rama, Surinam, Zanderij. ZSM: 2 ♂, Surinam.

*Pyrrhopyge amythaon polka* Evans, 1951. — RMNH: 1 ♂, 1 ♀, Kabalebo, Republiek.

*Pyrrhopyge sergius semana* Evans, 1951. — Evans (1951). ITZ: 2 ♀, Paramaribo, Surinam. RMNH: 2 ♂, 2 ♀, Bakhuisgebergte, Brownsberg, Republiek, Surinam.

*Pyrrhopyge charybdis semita* Evans, 1951. — RMNH: 1 ♂, Surinam. See Note 2.

*Pyrrhopyge amyclas amyclas* Cramer, 1779. — Cramer (1779); Evans (1951); Fabricius (1793, "Hesperia amiatus"); Möschler (1876); Williams & Bell (1931). ITZ: 3 ♂, 5 ♀, Paramaribo, Surinam. RMNH: 13 ♂, 12 ♀, Paramaribo, Surinam, Wageningen (at light), Zorg en Hoop. ZSM: 1 ♂, Surinam.

*Pyrrhopyge arinas arinas* Cramer, 1779. — Cramer (1779). RMNH: 1 ♂, Surinam (holotype).

*Pyrrhopyge creusae* Bell, 1931. — RMNH: 1 ♂, Sipaliwini.

*Pyrrhopyge rubricollis* Sepp, 1841. — Sepp (1841). RMNH: 1 ♀, Surinam.

*Pyrrhopyge cometes standingeri* Plötz, 1879. — Cramer (1779). RMNH: 1 ♂, Surinam. See Note 3.

*Elbella intersecta intersecta* Herrich-Schäffer, 1869. — RMNH: 1 ♀, Charlesburg.

*Elbella patrobas blanda* Evans, 1951. — Evans (1951). RMNH: 1 ♂, 1 ♀, Domburg.

*Elbella bicuspidis* spec. nov. — See Note 4.

*Elbella alburna* Mabille, 1891. — RMNH: 1 ♂, Voltzberg.

*Nosphistia zonara* Hewitson, 1866. — Möschler

(1876); possibly confused with a species of *Jemadia* or *Elbella*.

*Jemadia hospita ulixes* Plötz, 1879. — Evans (1951); Möschler (1882); Plötz (1879). ITZ: 1 (without abdomen), Surinam. RMNH: 1 ♀, Surinam.

*Jemadia menechmus* Mabille, 1878. — Evans (1951).

*Jemadia bewitsonii bewitsonii* Mabille, 1878. — RMNH: 2 ♂, 2 ♀, Brownsberg, Domburg, Surinam.

*Jemadia gnetus* Fabricius, 1781. — Cramer (1779, "Papilio vulcanus"); Evans (1951). RMNH: 1 ♀, Surinam.

*Jemadia fallax fallax* Mabille, 1878. — RMNH: 4 ♂, Coeroeni, Coppename, Zanderij. See Note 5.

*Amenis ponia ponina* Herrich-Schäffer, 1869. — ITZ: 1 (without abdomen), Surinam.

*Mysoria barcastus barcastus* Sepp, 1851. — Cramer (1775, "Papilio acastus"); Evans (1951); Möschler (1876, "Pyrrhopyge acastus"; 1882, "Pyrrhopyge barcastus" and "Pyrrhopyge acastus"); Sepp (1851); Williams & Bell (1931). ITZ: 6 ♂, 3 ♀, Surinam. RMNH: 28 ♂, 11 ♀, Belwaarde, Marienburg, Moengotapoe-Wiawia, Paramaribo, Surinam, Zorg en Hoop. ZSM: 2 ♂, Surinam.

*Mysoria thusus thusus* Stoll, 1781. — Stoll (1781). RMNH: 2 ♂, 1 ♀, Surinam.

*Myscelus nobilis* Cramer, 1779. — Cramer (1779); Evans (1951); Fabricius (1781, "Papilio salus").

*Myscelus assaricus assaricus* Cramer, 1779. — Cramer (1779); Möschler (1876). RMNH: 2 ♀, Surinam.

*Passova glacia* Evans, 1951. — Evans (1951).

*Passova passova stacer* Evans, 1951. — Evans (1951). RMNH: 1 ♂, Surinam. ZSM: 1 ♂, Surinam.

*Aspittha aspittha parima* Plötz, 1886. — Plötz (1886).

### Pyrginae

*Phocides palemon palemon* Cramer, 1779. — Cramer (1779); Evans (1952, "Phocides polybius polybius" Fabricius, 1793); Möschler (1876). ITZ: 1 ♀, Paramaribo. NZC: 1 ♀, Paramaribo. RMNH: 1 ♂, 9 ♀, Boniface, Carolina Creek, Paramaribo, Surinam (including holotype, ♂, of *Papilio palemon* Cramer).

*Phocides metrodorus* Bell, 1932. — NZC: 1 ♀, Republiek. RMNH: 1 ♂, Domburg.

*Phocides pigmalion hewitsonius* Mabille, 1883. — Möschler (1876, "Erycides pygmalion Cr."); determination uncertain, as he gave as synonym "Gnetus Ltrll.", which belongs to *Jemadia*. NZC: 1 ♀, Zorg en Hoop. RMNH: 2 ♂, 2 ♀, Paramaribo, Surinam. See Note 6.

*Phocides lincea lincea* Herrich-Schäffer, 1869. — RMNH: 1 ♀, Charlesburg.

*Tarsocstenus papias* Hewitson, 1857. — Williams & Bell (1931).

*Tarsocstenus corythus* Cramer, 1777. — Cramer (1777); Stoll (1782, "Papilio pyramus"). RMNH: 2 ♀, Surinam (including holotype of *Papilio corythus* Cramer). ZSM: 1 ♂, 2 ♀, Surinam.

*Tarsocstenus praecia rufibasis* Mabille, 1910. — RMNH: 4 ♂, 1 ♀, Carolina Creek, Surinam, Zanderij. ZSM: 1 ♂, Surinam.

*Phanus vitreus* Stoll, 1781. — Evans (1952); Möschler (1876, 1882); Stoll (1781); Williams & Bell (1931). RMNH: 1 ♂, 3 ♀, Avanavero Vallen, Carolina Creek, Voltzberg. ZSM: 1 ♂, Surinam.

*Phanus obscurior* Kaye, 1924. — Evans (1952).

*Phanus marshallii* Kirby, 1880. — Evans (1952). RMNH: 9 ♀, Avanavero Vallen, Brownsberg, Carolina Creek, Jodensavanne, Rama, Surinam. ZSM: 3 ♂, 3 ♀, Surinam.

*Udranomia orcinus* Felder, 1876. — Möschler (1876).

*Udranomia kikkawai* Weeks, 1906. — ZSM: 1 ♀, Surinam.

*Drephalys phoenice* Hewitson, 1867. — Möschler (1882). ZSM: 1 ♀, Surinam.

*Drephalys dumeril* Latreille, 1824. — Evans (1952); Möschler (1876).

*Drephalys oriander* *oriander* Hewitson, 1867. — Evans (1952). RMNH: 1 ♀, Goliath Creek.

*Drephalys talboti* Le Cerf, 1922. — Evans (1952).

*Drephalys opifex* Evans, 1952. — Evans (1952).

*Drephalys alcmon* Cramer, 1779. — Cramer (1779); Evans (1952); Möschler (1876). RMNH: 1 ♀, Zanderij. ZSM: 1 ♂, 1 ♀, Surinam.

*Augiades crinus* Cramer, 1780. — Cramer (1780); Evans (1952); Möschler (1882); Williams & Bell (1931). ITZ: 1 ♂, 4 ♀, Paramaribo, Surinam, Zanderij. NZC: 1 ♂, Paramaribo. RMNH: 5 ♂, 2 ♀, Lelydorp, Moengo, Paramaribo, Rama, Zanderij. ZSM: 2 ♂, 3 ♀, Surinam.

*Hyalothryrus infernalis* *infernalis* Möschler,

1876. — Evans (1952); Möschler (1876). RMNH: 8 ♂, 3 ♀, Avanavero Vallen, Carolina Kreek, Fallawatra Kreek, Goliath Kreek, Hebiwerie, Lely Gebergte, Raleigh Vallen (Voltzberg), Rama, Sipaliwini.
- Hyalothyrus leucomelas* Geyer, 1832. — Möschler (1876). RMNH: 1 ♂, 1 ♀, Avanavero Vallen. ZSM: 1 ♂, Surinam.
- Hyalothyrus nitocris* Stoll, 1782. — Evans (1952); Möschler (1882); Stoll (1782); Williams & Bell (1931). ITZ: 1 ♂, Surinam. RMNH: 5 ♂, 3 ♀, Goliath Kreek, Rama, Zanderij. ZSM: 11 ♂, 4 ♀, Surinam.
- Hyalothyrus neleus pempygargyra* Mabille, 1888. — Evans (1952); Möschler (1882). RMNH: 1 ♂, Coppename (Kroetoe).
- Phareas coeleste* Westwood, 1852. — Evans (1952); Williams & Bell (1931). RMNH: 2 ♂, Sipaliwini. ZSM: 2 ♀, Surinam.
- Entheus eumelus* Cramer, 1777. — Cramer (1777); Williams & Bell (1931, "Entheus mina"). RMNH: 1 ♀, Goliath Kreek. ZSM: 1 ♂, Surinam (lacks the costal fold).
- Entheus gentius* Cramer, 1779. — Cramer (1779); Evans (1952); Möschler (1882); Williams & Bell (1931). ITZ: 1 ♂, Surinam. RMNH: 3 ♂, 9 ♀, Avanavero Vallen, Blakawatra, Goliath Kreek, Lely Gebergte, Phe-dra, Rama, Republiek, Zanderij. ZSM: 5 ♂, 5 ♀, Surinam. See Note 7.
- Entheus priassus* Linnaeus, 1758. — Evans (1952); Möschler (1876, "Entheus talaus L." and "Entheus peleus L."); Stoll (1782); Williams & Bell (1931). ITZ: 3 ♂, 1 ♀, Surinam. RMNH: 5 ♀, Albina, Avanavero Vallen, Brownsberg, Surinam, Zanderij. ZSM: 10 ♂, 5 ♀, Surinam.
- Entheus matho dius* Mabille, 1897. — Evans (1952). RMNH: 5 ♂, 1 ♀, Kabelstation, Kroetoe, Ramam, Surinam, Zanderij.
- Cabirus procas* Cramer, 1777. — Cramer (1777); Evans (1952); Stoll (1787, "Papilio julettus"). RMNH: 2 ♂, Copi, Lely Gebergte.
- Proteides mercurius mercurius* Fabricius, 1787. — Cramer (1779, "Papilio idas"); Möschler (1882, "Thymele idas Cr."); Sepp (1848, "Papilio idas Cramer"). ITZ: 2 ♂, Surinam. RMNH: 1 ♂, Oele mari.
- Epargyreus clarus* Cramer, 1775. — Cramer (1775; described from Surinam, but locality undoubtedly false, the species is not known to occur south of Honduras); Evans (1952; locality not trusted by Evans).
- Epargyreus socus sinus* Evans, 1952. — Evans (1952).
- Epargyreus exadens* Cramer, 1779. — Cramer (1779); Möschler (1882). RMNH: 1 ♂, Surinam. ZSM: 1 ♂, Surinam.
- Polygonus leo* Gmelin, 1790. — Evans (1952). ITZ: 2 ♂, Surinam.
- Chioides catillus catillus* Cramer, 1779. — Cramer (1779); Evans (1952); Möschler (1876); Sepp (1847, "Papilio longicauda"); Williams & Bell (1931). ITZ: 2 ♂, 2 ♀, Paramaribo, Surinam. RMNH: 18 ♂, 11 ♀, Albina, Bigiston, Blauwgrond, Brokopondo, Coppename Rivier, Goliath Kreek, Lelydorp, Ma Retraite, Onverdacht, Paramaribo, Tibiti. ZSM: 4 ♂, 1 ♀, Surinam.
- Aguna asander asander* Hewitson, 1867. — Evans (1952).
- Aguna claxon* Evans, 1952. — RMNH: 1 ♂, Brownsberg. See Note 8.
- Aguna aurunce* Hewitson, 1867. — RMNH: 1 ♂, 1 ♀, Brokopondo, Carolina Kreek.
- Aguna coelus* Stoll, 1781. — Evans (1952); Möschler (1876); Stoll (1781). RMNH: 2 ♀, Lely Gebergte, Rama. ZSM: 2 ♀, Surinam.
- Aguna ganna* Möschler, 1878. — Evans (1952); Williams & Bell (1931).
- Typhedanus orion* Cramer, 1779. — Cramer (1779); Evans (1952); Möschler (1882); Williams & Bell (1931). ITZ: 1 ♂, 2 ♀, Paramaribo, Surinam. RMNH: 10 ♂, 4 ♀, Carolina Kreek, Domburg, Lelydorp, Paramaribo.
- Typhedanus undulatus* Hewitson, 1867. — Evans (1952); Möschler (1876). ITZ: 2 ♂, 1 ♀, Paramaribo, Surinam. RMNH: 3 ♂, 4 ♀, Ma Retraite, Paramaribo, Zorg en Hoop. ZSM: 1 ♂, Surinam.
- Typhedanus optica optica* Evans, 1952. — RMNH: 1 ♂, 2 ♀, Brokopondo. ZSM: 1 ♂, Surinam.
- Polythrix octomaculata octomaculata* Sepp, 1844. — Möschler (1882); Sepp (1844). RMNH: 1 ♂, 5 ♀, Paramaribo. ZSM: 1 ♂, Surinam.
- Polythrix asine* Hewitson, 1867. — RMNH: 1 ♀, Paramaribo. See Note 9.
- Polythrix minvanes* Williams, 1926. — ZSM: 1 ♂, Surinam.
- Polythrix caunus* Herrich-Schäffer, 1869. — Evans (1952). RMNH: 4 ♂, 2 ♀, Brokopondo, Paramaribo, Rama, Republiek. See Note 10.
- Polythrix auginus* Hewitson, 1867. — Evans (1952); Möschler (1876). ZSM: 1 ♂, Surinam.

- Polythrix metallescens* Mabille, 1888. — RMNH: 3 ♂, 1 ♀, Ma Retraite, Republiek, Surinam.
- Polythrix eudoxus* Stoll, 1781. — Stoll (1781).
- Chrysoplectrum pervivax* Hübner, 1819. — Evans (1952); Hübner (1819); Kirby (1871, "Pamphila schellerti"); Möschler (1876, "Telegonus schellerti Kirby"); Sepp (1832—1840, "Papilio pertinax Stoll"); Stoll (1790, "Papilio pertinax"); Williams & Bell (1931). RMNH: 2 ♀, Leonsberg, Paramaribo.
- Chrysoplectrum bahiana bahiana* Herrich-Schäffer, 1869. — Evans (1952). RMNH: 2 ♂, Paramaribo, Surinam.
- Chrysoplectrum otiades* Hewitson, 1867. — RMNH: 2 ♂, Brownsberg.
- Chrysoplectrum perniciosus perniciosus* Herrich-Schäffer, 1869. — Evans (1952). RMNH: 1 ♂, 2 ♀, Brownsberg, Paramaribo.
- Chrysoplectrum orpheus* Plötz, 1882. — ZSM: 1 ♂, Surinam.
- Urbanus proteus* Linnaeus, 1758. — Evans (1952); Möschler (1876); Williams & Bell (1931). ITZ: 2 ♂, 7 ♀, Caledonia-Saramacca, Paramaribo, Surinam. RMNH: 8 ♂, 9 ♀, Albina, Marienburg, Paramaribo, Raleigh Vallen. ZSM: 1 ♂, Surinam.
- Urbanus viterboana alva* Evans, 1952. — Evans (1952). NZC: 1 ♂, Charlesburg. RMNH: 1 ♂, 4 ♀, Brokopondo, Paramaribo, Sipaliwini.
- Urbanus esmeraldus* Butler, 1877. — Evans (1952). RMNH: 1 ♂, Surinam.
- Urbanus esma* Evans, 1952. — RMNH: 2 ♂, Ma Retraite, Zanderij. See Note 11.
- Urbanus esta* Evans, 1952. — RMNH: 1 ♂, Domburg (agrees with *esta*, but valves symmetrical, both like Evans' figure of right valve). ZSM: 1 ♀, Surinam.
- Urbanus acawoios* Williams, 1926. — Evans (1952). ITZ: 1 ♂, Paramaribo. RMNH: 1 ♀, Lelydorp. ZSM: 1 ♀, Surinam.
- Urbanus dorantes dorantes* Stoll, 1790. — Evans (1952); Möschler (1882); Stoll (1790); Williams & Bell (1931). ITZ: 2 ♀, Surinam. RMNH: 11 ♂, 10 ♀, Albina, Ma Retraite, Paramaribo. ZSM: 2 ♂, 1 ♀, Surinam.
- Urbanus teleius* Hübner, 1821. — Evans (1952); Möschler (1876); Williams & Bell (1931, "Goniurus eurycles Latr."). RMNH: 8 ♂, 6 ♀, Domburg, Onverdacht, Paramaribo, Zanderij-Saramacca.
- Urbanus tanna* Evans, 1952. — Evans (1952).
- Urbanus cindra* Evans, 1952. — RMNH: 1 ♂, Copi.
- Urbanus ambiguus* spec. nov. — See Note 12.
- Urbanus zagorus* Plötz, 1881. — RMNH: 1 ♂, Surinam. Unlikely locality; only known from S. Brazil and Argentina.
- Urbanus simplicius* Stoll, 1790. — Evans (1952); Möschler (1876, 1882); Stoll (1790); Williams & Bell (1931). ITZ: 7 ♂, 4 ♀, Paramaribo, Surinam. RMNH: 38 ♂, 17 ♀, Albina, Avanavero Vallen, Bigiston, Brokopondo, Brownsberg, Charlesburg, Domburg, Groningen, Lelydorp, Ma Retraite, Paramaribo, Republiek, Zanderij, Zorg en Hoop. ZSM: 1 ♂, Surinam.
- Urbanus procne* Plötz, 1881. — Evans (1952). ITZ: 4 ♂, 2 ♀, Charlesburg, Paramaribo. NZC: 2 ♂, 2 ♀, Paramaribo. RMNH: 42 ♂, 17 ♀, Charlesburg, Cultuurtuin, Domburg, Kabelstation, Kwatta, Lelydorp, Ma Retraite, Paramaribo, Republiek.
- Urbanus doryssus doryssus* Swainson, 1831. — Evans (1952); Möschler (1876); Williams & Bell (1931). ITZ: 1 ♂, 1 ♀, Surinam. NZC: 1 ♂, Benzcorp. RMNH: 5 ♂, Brownsberg, Corantijn Rivier, Domburg, Paramaribo. ZSM: 5 ♂, 4 ♀, Surinam.
- Urbanus albimargo takuta* Evans, 1952. — Evans (1952); Williams & Bell (1931). RMNH: 2 ♀, Avanavero Vallen, Brownsberg. ZSM: 1 ♂, Surinam.
- Urbanus virescens* Mabille, 1877. — ZSM: 1 ♂, Surinam.
- Astraptes talus* Cramer, 1777. — Cramer (1777); Möschler (1876); Sepp (1841, "Papilio lucidator"). ITZ: 1 ♀, Paramaribo. RMNH: 4 ♂, 4 ♀, Albina, Carolina Kreek, Leonsberg, Paramaribo, Surinam. ZSM: 1 ♀, Surinam.
- Astraptes fulgerator fulgerator* Walch, 1775. — Evans (1952); Möschler (1876); Sepp (1841, "Papilio fulminator"); Williams & Bell (1931). ITZ: 1 ♀, Surinam. RMNH: 4 ♂, 7 ♀, Brownsberg, Domburg, Ephraïms Zegen, Kabalebo/Corantijn Rivier, Lely Gebergte, Paramaribo, Surinam. ZSM: 3 ♂, 5 ♀, Surinam.
- Astraptes apastus apastus* Cramer, 1777. — Cramer (1777); Evans (1952). ITZ: 1 ♂, 1 ♀, Surinam. RMNH: 1 ♂, 1 ♀, Domburg, Surinam. ZSM: 1 ♂, Surinam.
- Astraptes enotrus* Stoll, 1781. — Stoll (1781). RMNH: 1 ♂, Rama. ZSM: 1 ♂, Surinam.
- Astraptes granadensis* Möschler, 1878. — Evans (1952); Möschler (1882); Stoll (1780, "Papilio aulestes"). ITZ: 1 ♂, Surinam. RMNH: 1 ♂, Surinam. ZSM: 1 ♂, Surinam.

- Astraptes narcosius* Stoll, 1790. — Evans (1952); ssp. *narcosius* and ssp. *aulina* Evans, 1952); Stoll (1790). RMNH: 1 ♂, Surinam (ssp. *narcosius*).  
*Astraptes alardus* Stoll, 1790. — Evans (1952); Möschler (1876); Stoll (1790). ITZ: 3 ♀, Domburg, Paramaribo, Surinam. RMNH: 6 ♂, 6 ♀, Charlesburg, Domburg, Paramaribo.  
*Astraptes alector hopfferi* Plötz, 1882. — Möschler (1882, "Thymele hopfferi Plötz"). RMNH: 2 ♂, 1 ♀, Brownsberg, Lucie Rivier, Rama.  
*Astraptes cretatus* Hayward, 1939. — RMNH: 1 ♂, 1 ♀, Carolina Kreek, Rama. See Note 13.  
*Astraptes creteus creteus* Cramer, 1780. — Cramer (1780); Evans (1952); Möschler (1876, "Teleonus parmenides" Cramer"; 1882, previous record was based on misidentification, referred to "Thymele Hopfferi"); Stoll (1781, "Papilio parmenides"). ITZ: 1 ♀, Surinam. NZC: 2 ♂, Phedra.  
*Astraptes latimargo* Herrich-Schäffer, 1869. — Möschler (1882); Williams & Bell (1931).  
*Astraptes chiriquensis oenander* Hewitson, 1876. — ZSM: 1 ♂, Surinam.  
*Astraptes anaphus anaphus* Cramer, 1777. — Cramer (1777); Evans (1952); Sepp (1830, "Papilio leucogramma"). ITZ: 1 ♀, Surinam. RMNH: 1 ♂, 3 ♀, Brokopondo, Surinam (including ♂ holotype, Surinam).  
*Calliades zeutus* Möschler, 1878. — ZSM: 1 ♀, Surinam.  
*Autochton neis* Geyer, 1832. — Evans (1952); Möschler (1876, "Cecropterus bocus Hopffer"); Williams & Bell (1931, "Cecropterus neis" Geyer" and "Cecropterus bocus Plötz"). ITZ: 1 ♂, Surinam. RMNH: 3 ♂, Domburg, Surinam. ZSM: 1 ♀, Surinam.  
*Autochton longipennis* Plötz, 1882. — Williams & Bell (1931, "Cecropterus capys (Godman & Salvin)". ITZ: 1 ♀, Surinam. RMNH: 5 ♂, Brownsberg, Domburg, Sipaliwini, Surinam. ZSM: 1 ♂, Surinam.  
*Autochton zarex* Hübner, 1818. — Hübner (1818); Möschler (1876); Williams & Bell (1931, "Cecropterus auna" Fabricius"). RMNH: 9 ♂, 3 ♀, Albina, Brownsberg, Carolina Kreek, Paramaribo, Surinam, Zanderij. ZSM: 1 ♂, 3 ♀, Surinam.  
*Autochton bipunctatus* Gmelin, 1790. — Möschler (1876). RMNH: 1 ♀, Albina.  
*Autochton itylus* Hübner, 1823. — Evans (1952); Hübner (1823). RMNH: 1 ♂, 1 ♀,  
Brownsberg, Paramaribo. ZSM: 3 ♂, 2 ♀, Surinam.  
*Thorybes daunus* Cramer, 1777. — Cramer (1777); apparently wrong locality for this strictly North American species.  
*Bungalotis erythrus* Cramer, 1775. — Cramer (1775). RMNH: 1 ♀, Kabalebo (at black light).  
*Bungalotis diophorus* Möschler, 1882. — Möschler (1882).  
*Bungalotis midas* Cramer, 1775. — Cramer (1775); Evans (1952); Fabricius (1781); Möschler (1876); Plötz (1882a). NZC: 1 ♀, Alalapaoe. RMNH: 2 ♂, 2 ♀, Cultuurtuin, Paramaribo, Sarakreek. ZSM: 1 ♂, Surinam.  
*Bungalotis astylos* Cramer, 1780. — Cramer (1780); Möschler (1876). RMNH: 1 ♂, 1 ♀, Paloemeu, Surinam. ZSM: 1 ♂, Surinam.  
*Bungalotis borax* Evans, 1952. — RMNH: 1 ♂, 1 ♀, Nassau Gebergte, Saramacca Rivier.  
*Bungalotis sipa* spec. nov. — See Note 14.  
*Bungalotis quadratum* Sepp, 1845. — Evans (1952); Möschler (1876, "Teleonus annulicornis"); Sepp (1845). NZC: Paramaribo. RMNH: 1 ♂, 1 ♀, Paramaribo, Saramacca Rivier. See Note 15.  
*Salatis salatis* Stoll, 1782. — Evans (1952); Plötz (1882a); Stoll (1782). RMNH: 1 ♂, 2 ♀, Ephraïms Zegen, Lely Gebergte, Onverdacht.  
*Salatis cebrenus* Cramer, 1777. — Cramer (1777).  
*Salatis fulvius* Plötz, 1882. — RMNH: 1 ♀, Wonotobo.  
*Salatis flavomarginatus* Sepp, 1851. — Sepp (1851).  
*Sarmientoia eriopis* Hewitson, 1867. — Evans (1952). RMNH: 1 ♀, Onverdacht.  
*Dyscophellus euribates* Stoll, 1782. — Evans (1952); Möschler (1876, "Teleonus hesus Westwood"); Stoll (1782). RMNH: 3 ♂, 1 ♀, Goliath Kreek (at light), Saramacca Rivier, Surinam. ZSM: 2 ♂, Surinam.  
*Dyscophellus porcius* Felder, 1862. — Evans (1952); Möschler (1882, "Thymele doriscus Hewitson").  
*Dyscophellus sebaldus* Stoll, 1781. — Evans (1952); Stoll (1781). RMNH: 2 ♀, Sipaliwini (at light), Surinam.  
*Dyscophellus erythras* Mabille, 1888. — Evans (1952).  
*Dyscophellus diaphorus* Mabille & Bouillet, 1912. — Mabille & Bouillet (1912).  
*Dyscophellus ramusis* Stoll, 1781. — Evans (1952); Möschler (1876, 1882); Stoll (1781).

NZC: 1 ♀, Kabo. RMNH: 2 ♂, 1 ♀, Afobaka, Goliath Kreek, Surinam.

*Nascus phocus* Cramer, 1777. — Cramer (1777); Möschler (1876, "Telegonus pherenice Hewitson"); Sepp (1843, "Papilio decemmaculata"); Stoll (1782, "Papilio morpheus"). NZC: 1 ♀, Paramaribo. RMNH: 2 ♂, 1 ♀, Domburg, Paramaribo, Surinam.

*Nascus solon* Plötz, 1882. — RMNH: 1 ♀, Surinam.

*Nascus broteas* Cramer, 1780. — Cramer (1780). ZSM: 2 ♂, Surinam.

*Nascus paulliniae* Sepp, 1842. — Evans (1952); Sepp (1842). RMNH: 1 ♂, 1 ♀, Domburg, Paramaribo (at light). ZSM: 2 ♂, Surinam.

*Cephise cephise* Herrich-Schäffer, 1869. — Evans (1952); Möschler (1876).

*Porphyrogenes passalus* *passalus* Herrich-Schäffer, 1869. — RMNH: 1 ♂, Rama.

*Porphyrogenes probus* Möschler, 1876. — Möschler (1876).

*Porphyrogenes zohra* Möschler, 1878. — RMNH: 1 ♂, Coppename Rivier.

*Porphyrogenes pausias* Hewitson, 1867. — RMNH: 1 ♂, Zanderij. ZSM: 1 ♂, Surinam.

*Ablepsis azines* Hewitson, 1867. — Mabille & Boullet (1912, "Telemiades perseus"). RMNH: 1 ♀, Zanderij. ZSM: 1 ♂, 1 ♀, Surinam.

*Orneatus aegiochus* Hewitson, 1876. — Möschler (1882), probably confused with an *Astrape* species, *O. aegiochus* being known from C. America only.

*Celaenorrhinus shema shema* Hewitson, 1877. — Evans (1952); Möschler (1882, "Plesioneuria ochrogutta").

*Celaenorrhinus similis bifurcus* Bell, 1934. — Evans (1952).

*Celaenorrhinus* spec. nov. — Will be described in a separate paper.

*Celaenorrhinus eligius eligius* Stoll, 1782. — Evans (1952); Stoll (1782); Williams & Bell (1931).

*Celaenorrhinus syllius* Felder, 1862. — Evans (1952). RMNH: 1 ♀, Brownsberg.

*Spathilepia clonius* Cramer, 1775. — Evans (1953); Möschler (1876); Williams & Bell (1931). RMNH: 7 ♂, 3 ♀, Brokopondo, Domburg, Paramaribo.

*Cogia hassan* Butler, 1870. — Williams & Bell (1931, "Cogia freudiae"). RMNH: 13 ♂, 6 ♀, Temomairem, Zanderij. See Note 16.

*Cogia calchas* Herrich-Schäffer, 1869. — Möschler (1876). RMNH: 2 ♂, 1 ♀, Brokopondo, Rama.

*Telemiades vansa* Evans, 1953. — ZSM: 6 ♀, Surinam.

*Telemiades squanda* Evans, 1953. — RMNH: 1 ♀, Brokopondo.

*Telemiades trenda* Evans, 1953. — Evans (1953).

*Telemiades nicomedes* Möschler, 1878. — Evans (1953).

*Telemiades epicalus* Hübner, 1819. — Evans (1953).

*Telemiades penidas* Hewitson, 1876. — Möschler (1876, "Teleonus mygdon"); Williams & Bell (1931, "Telemiades ceramina Herrich-Schäffer"). RMNH: 1 ♂, 1 ♀, Brokopondo, Brownsberg.

*Telemiades avitus* Stoll, 1781. — Stoll (1781); Williams & Bell (1931).

*Telemiades amphion amphion* Hübner, 1826. — Möschler (1876, "Plesioneura compressa"); Williams & Bell (1931). ITZ: 1 ♀, Surinam. RMNH: 3 ♂, 2 ♀, Domburg, Rama, Sipaliwini.

*Pyrdalus corbulo* Stoll, 1781. — Möschler (1876); Stoll (1781). RMNH: 1 ♂, Surinam. ZSM: 1 ♂, 1 ♀, Surinam.

*Ectomis cythna* Hewitson, 1878. — Evans (1953). RMNH: 1 ♀, Brokopondo (the first known female of this scarce species).

*Conognathus platon* Felder, 1862. — RMNH: 1 ♂, Saramacca Rivier.

*Arteurotia tractipennis* Butler & Druce, 1872. — Evans (1953).

*Eracon paulinus* Stoll, 1782. — Stoll (1782). RMNH: 1 ♀, Lely Gebergte.

*Eracon onorbo* Möschler, 1882. — Evans (1953); Möschler (1882).

*Spioniades artemides* Stoll, 1782. — Evans (1953); Möschler (1876); Stoll (1782). RMNH: 1 ♀, Zanderij. ZSM: 2 ♂, Surinam.

*Spioniades libethra* Hewitson, 1868. — Evans (1953).

*Polyctor polyctor* Prittwitz, 1868. — RMNH: 1 ♂, Zanderij. ZSM: 1 ♀, Surinam.

*Nisoniades bessus* Möschler, 1876. — Evans (1953); Möschler (1876). RMNH: 4 ♂, Brokopondo, Paramaribo, Zanderij.

*Nisoniades laurentina* Williams & Bell, 1939. — RMNH: 1 ♂, Brokopondo.

*Nisoniades rubescens* Möschler, 1876. — Evans (1953); Möschler (1876); Williams & Bell (1931, "Pellicia bromias Godman & Salvini"). RMNH: 5 ♂, Domburg, Ma Retraite, Paramaribo.

*Nisoniades mimas* Cramer, 1775. — Cramer (1775); Evans (1953); Sepp (1845, "Papilio

- bromius* Stoll"); Stoll (1790, "Papilio *bromius*"). RMNH: 1 ♂, Sipaliwini.
- Nisoniades ephora* Herrich-Schäffer, 1870. — Möschler (1882).
- Nisoniades rimana* Bell, 1942. — RMNH: 1 ♂, Brownsberg. ZSM: 1 ♂, Surinam.
- Nisoniades brunneata* Williams & Bell, 1939. — Evans (1953).
- Nisoniades macarius* Herrich-Schäffer, 1870. — Williams & Bell (1931). NZC: 1 ♂, Alaman-didon.
- Pachyneuria duidae* Bell, 1932. — Evans (1953).
- Pellicia dimidiata* Herrich-Schäffer, 1870. — Möschler (1876, "Pellicia *didia*").
- Morvina fissimacula rema* Evans, 1953. — ZSM: 1 ♀, Surinam.
- Myrinia binoculus* Möschler, 1876. — Möschler (1876).
- Cyclosemia herennius* Stoll, 1782. — Evans (1953); Stoll (1782).
- Viola violella* Mabille, 1897. — Evans (1953). RMNH: 2 ♂, 1 ♀, Paramaribo.
- Plumbago plumbago* Plötz, 1884. — RMNH: 1 ♀, Paramaribo.
- Gorgythion begga pyralina* Möschler, 1876. — Evans (1953); Möschler (1876, "Nisoniades *plautia*" and "Helias *pyralina*"); Williams & Bell (1931). NZC: 1 ♀, Potribo. RMNH: 1 ♂, Zanderij. ZSM: 1 ♀, Surinam.
- Gorgythion beggina escalophoides* Hayward, 1941. — RMNH: 6 ♂, 6 ♀, Brokopondo, Domburg, Paramaribo.
- Gorgythion canda* Evans, 1953. — ZSM: 1 ♀, Surinam. Identification must remain preliminary, as long as female genitalia of *Gorgythion* species have not been studied.
- Ouleus matria dampa* Evans, 1953. — ZSM: 1 ♀, Surinam.
- Ouleus fridericus fridericus* Geyer, 1832. — Evans (1953); Möschler (1876); Williams & Bell (1931). RMNH: 8 ♂, 1 ♀, Albina, Domburg, Ma Retraite, Paloemeu, Paramaribo, Surinam.
- Zera tetrastigma* Sepp, 1847. — Sepp (1847). RMNH: 1 ♀, Blakawatra.
- Quadrus cerealis* Stoll, 1782. — Evans (1953, "cerealis", incorrect subsequent spelling); Möschler (1876); Sepp (1847); Stoll (1782); Williams & Bell (1931). ITZ: 2 ♂, 2 ♀, Paramaribo, Surinam. RMNH: 8 ♂, 6 ♀, Avanavero Vallen, Lely Geberge, Ma Retraite, Paramaribo, Surinam. ZSM: 1 ♂, 3 ♀, Surinam.
- Quadrus fanda* Evans, 1953. — ZSM: 1 ♂, Surinam.
- Quadrus contubernalis* Mabille, 1883. — RMNH: 3 ♂, Blakawatra, Brownsberg. ZSM: 1 ♀, Surinam.
- Quadrus deyrolli deyrolli* Mabille, 1877. — Evans (1953). RMNH: 2 ♂, 1 ♀, Brownsberg, Copi, Zanderij. ZSM: 6 ♂, Surinam.
- Gindanes brebissoni* Latreille, 1824. — RMNH: 1 ♀, Carolina Kreek. Comes closest to ssp. *phagesia* Hewitson, 1868.
- Pythonides jovianus jovianus* Stoll, 1782. — Evans (1953); Möschler (1876); Stoll (1782); Williams & Bell (1931). ITZ: 1 ♂, 1 ♀ Surinam. RMNH: 6 ♂, 7 ♀, Albina, Avanavero Vallen, Brownsberg, Lely Geberge, Nassau Geberge, Rama, Surinam, Zanderij, Zanderij-Matta. ZSM: 6 ♂, 4 ♀, Surinam.
- Pythonides lerina* Hewitson, 1868. — Evans (1953); Möschler (1876); Williams & Bell (1931). RMNH: 3 ♂, Rama, Surinam, Zanderij. ZSM: 6 ♂, 1 ♀, Surinam.
- Pythonides grandis assecla* Mabille, 1883. — RMNH: 2 ♂, Koffiekamp, Rama.
- Pythonides herennius herennius* Geyer, 1838. — ITZ: 1 ♂, Surinam. RMNH: 3 ♂, Surinam.
- Pythonides limaea limaea* Hewitson, 1868. — Evans (1953); Möschler (1882).
- Sosrata festiva* Erichson, 1848. — Evans (1953). ITZ: 1 ♂, Surinam. RMNH: 1 ♂, 1 ♀, Brokopondo, Surinam. ZSM: 1 ♂, Surinam.
- Sosrata bifasciata adamas* Plötz, 1884. — Evans (1953).
- Paches exosa* Butler, 1877. — Plötz (1884, "Pythonides *prudens*").
- Milanion hemes hemes* Cramer, 1777. — Cramer (1777); Evans (1953); Möschler (1876, 1882). ITZ: 1 ♂, Surinam. RMNH: 3 ♂, 3 ♀, Brokopondo, Brownsberg, Sipaliwini, Surinam, Zanderij.
- Milanion leucaspis* Mabille, 1878. — ZSM: 1 ♂, Surinam.
- Milanion pilumnus albidior* Mabille & Boullet, 1917. — ZMS: 1 ♂, Surinam.
- Paramimus scurra* Hübner, 1809. — Evans (1953); Möschler (1882, "Pythonides *leucoesma* Erichson"); Williams & Bell (1931). ITZ: 1 ♂, Surinam. RMNH: 5 ♂, 2 ♀, Albina, Blakawatra, Brownsberg, Surinam, Zanderij. ZSM: 1 ♂, 6 ♀, Surinam.
- Charidia lucaria lucaria* Hewitson, 1868. — Evans (1953); Williams & Bell (1931). RMNH: 1 ♀, Brownsberg. ZSM: 1 ♀, Surinam.
- Mylon menippus* Fabricius, 1776. — Cramer (1782, "Papilio *melander*"); Fabricius

- (1776); Möschler (1876, "Achlyodes melan-  
der Cramer"). ITZ: 1 ♂, Surinam. RMNH:  
2 ♀, Brownsberg.
- Mylon jason* Ehrmann, 1907. — Evans (1953);  
Williams & Bell (1931).
- Carrhenes fuscescens conia* Evans, 1953. —  
ZSM: 1 ♀, Surinam.
- Carrhenes canescens leada* Butler, 1860. —  
Evans (1953).
- Clito jonkersi* spec. nov. — See Note 17.
- Clito clito* Fabricius, 1787. — Möschler (1876).  
ZSM: 1 ♂, Surinam.
- Clito zenda* Evans, 1953. — Evans (1953).
- Xenophanes tryxus* Stoll, 1780. — Evans (1953);  
Möschler (1876); Stoll (1780); Williams &  
Bell (1931). ITZ: 2 ♂, Surinam. RMNH: 12  
♂, 5 ♀, Brokopondo, Brownsberg, Lely-  
dorp, Ma Retraite, Paramaribo, Sipaliwini,  
Surinam. ZSM: 2 ♂, Surinam.
- Antigonus erosus* Hübner, 1812. — Evans  
(1953); Möschler (1876, "Antigonus wester-  
manni Latreille"; 1882).
- Timochreon doria* Plötz, 1884. — RMNH: 1 ♀,  
Rama.
- Anisochoria pedalioidina polysticta* Mabille,  
1876. — Evans (1953).
- Achlyodes busirus* busirus Stoll, 1782. —  
Möschler (1882); Stoll (1782). RMNH: 3 ♂,  
1 ♀, Brownsberg, Surinam, Zanderij.
- Achlyodes thraso* thraso Jung, 1792. — Evans  
(1953); Möschler (1882); Williams & Bell  
(1931). NZC: 1 ♂, 1 ♀, Paramaribo.  
RMNH: 9 ♂, 6 ♀, Brownsberg, Ma Retraite,  
Paramaribo, Zanderij. ZSM: 1 ♂, Su-  
rinam.
- Anastrus sempiternus simplicior* Möschler, 1876.  
— Möschler (1876). RMNH: 1 ♀, Ma Retraite.
- Anastrus tolimus robicus* Plötz, 1884. — Evans  
(1953). RMNH: 3 ♂, 4 ♀, Blakawatra, Bro-  
kopondo, Paramaribo, Patamakka Rivier,  
Surinam.
- Anastrus petius* Möschler, 1876. — Evans  
(1953); Möschler (1876). ZSM: 5 ♂, 2 ♀, Su-  
rinam.
- Anastrus obliqua* Plötz, 1884. — RMNH: 1 ♀,  
Zanderij.
- Anastrus obscurus narva* Evans, 1953. — Evans  
(1953). ITZ: 3 ♂, 2 ♀, Paramaribo, Surinam.  
RMNH: 3 ♂, 2 ♀, Brokopondo, Lelydorp,  
Matapi. ZSM: 1 ♂, 2 ♀, Surinam.
- Ebrietas infanda* Butler, 1876. — RMNH: 1 ♀,  
Brownsberg.
- Cycloglypha thrasibus* thrasibus Fabricius,  
1793. — Evans (1953). RMNH: 1 ♂, 2 ♀,  
Brokopondo, Rama, Surinam. ZSM: 1 ♂,  
Surinam.
- Cycloglypha caeruleonigra* Mabille, 1904. —  
RMNH: 2 ♂, Paramaribo, Sipaliwini.
- Cycloglypha enega* Möschler, 1876. —  
Möschler (1876). RMNH: 2 ♂, 1 ♀, Broko-  
ponto, Paloemeu, Paramaribo.
- Helias phalaenoides phalaenoides* Fabricius,  
1807. — Evans (1953); Williams & Bell  
(1931). ITZ: 1 ♂, Surinam. RMNH: 1 ♂, 3  
♀, Brownsberg, Coeroeni Eiland, Surinam.
- Chiomara asychis asychis* Stoll, 1780. — Evans  
(1953); Möschler (1876), "Pythonides diluci-  
da" and "Achlyodes asychis Cramer"; Stoll  
(1780); Williams & Bell (1931). RMNH: 8  
♂, 5 ♀, Belwaarde, Kwatta, Ma Retraite,  
Marienburg, Paramaribo, Surinam, Wia-wia.
- Chiomara mithrax* Möschler, 1878. — Evans  
(1953). RMNH: 1 ♀, Paramaribo.
- Chiomara punctum* Mabille, 1878. — Evans  
(1953); Williams & Bell (1931). RMNH: 1  
♂, 5 ♀, Copi, Ma Retraite, Zanderij. ZSM: 3  
♂, 2 ♀, Surinam.
- Ephyriades arcas philemon* Fabricius, 1775. —  
Möschler (1876, "Nisoniades otreus Cramer");  
Stoll (1780, "Papilio otreus", and  
"Papilio flyas"). RMNH: 1 ♂, Surinam.
- Pyrgus oileus orcus* Stoll, 1780. — Evans (1953);  
Hübner (1809, "Papilio tartarus"); Möschler  
(1876, "Hesperia syrichtus Fabricius"); Stoll  
(1780); Williams & Bell (1931). ITZ: 6 ♂, 4  
♀, Paramaribo, Surinam. RMNH: 35 ♂, 21  
♀, Benzendorp, Brokopondo, Coeroeni Eiland  
(in Coeroeni Rivier), Domburg, Kabelsta-  
tion, Kwatta, Ma Retraite, Paramaribo, Par-  
anam, Stoelmans Eiland (in Marowijne).  
Brown & Heineman (1972: 389) considered  
*orcus* specifically distinct from *oileus*, but evi-  
dence of real sympatry is not yet convinc-  
ing.
- Helioptetes arsalte arsalte* Linnaeus, 1758. —  
Evans (1953); Möschler (1882); Williams &  
Bell (1931). ITZ: 3 ♂, 2 ♀, Caledonia-Sara-  
macca, Paramaribo, South side Upper Sara-  
macca, Surinam. RMNH: 20 ♂, 9 ♀, Albina,  
Kayser Gebergte, Kwatta, Leiding, Lely-  
dorp, Maratakka, Paramaribo, Sipaliwini.  
ZSM: 5 ♂, 2 ♀, Surinam.
- Helioptetes leucola* Hewitson, 1868. — Möschler  
(1882), probably confused this rare Brazilian  
species with the next species, which is com-  
mon in Surinam.
- Helioptetes alana* Reakirt, 1868. — Evans

(1953). RMNH: 7 ♂, 2 ♀, Brokopondo, Goliath Kreek, Rama, Sipaliwini. ZSM: 1 ♀, Surinam.

### Hesperiinae

*Synapte silius* Latreille, 1824. — RMNH: 1 ♂, Domburg.

*Lento ferrago* Plötz, 1884. — RMNH: 1 ♀, Morico Kreek.

*Lento lento* Mabille, 1878. — ITZ: 1 ♂, Republiek.

*Zariaspes mys* Hübner, 1808. — Williams & Bell (1931). RMNH: 5 ♂, 5 ♀, Domburg, Lelydorp, Ma Retraite, Surinam.

*Anthoptus epictetus* Fabricius, 1793. — Evans (1955); Möschler (1882); Williams & Bell (1931). ITZ: 2 ♂, 1 ♀, Leiding, Paramaribo. RMNH: 15 ♂, 1 ♀, Brokopondo, Domburg, Goliath Kreek, Kayser Gebergte, Paramaribo, Rama, Sipaliwini, Surinam. See Note 18.

*Corticea corticea corticea* Plötz, 1883. — Evans (1955); Williams & Bell (1931, "Megistias noctis Plötz"). RMNH: 6 ♂, 3 ♀, Domburg, Ma Retraite, Paramaribo, Surinam, Zanderij.

*Cantha celeus* Mabille, 1891. — Williams & Bell (1931).

*Vinius tryhana* Kaye, 1913. — NZC: 1 ♂, Pepejoe. RMNH: 3 ♂, Domburg, Ma Retraite, Paramaribo. See Note 19.

*Molo mango* Guenée, 1865. — Evans (1955). RMNH: 3 ♂, Nassau Gebergte, Surinam. ZSM: 1 ♂, Surinam.

*Molo menta* Evans, 1955. — Evans (1955).

*Apaustus gracilis smarti* Evans, 1955. — Williams & Bell (1931). RMNH: 4 ♂, 1 ♀, Avanavero Vallen (Malaise trap), Raleigh Valen.

*Apaustus menes* Stoll, 1782. — Evans (1955); Möschler (1876); Sepp (1842); Williams & Bell (1931). RMNH: 3 ♂, Ma Retraite, Paramaribo. ZSM: 1 ♂, Surinam. See Note 20.

*Callimormus radiola radiola* Mabille, 1878. — Evans (1955); Williams & Bell (1931). RMNH: 3 ♂, 1 ♀, Brownsberg, Domburg.

*Callimormus alsimo* Möschler, 1882. — Möschler (1882). ZSM: 1 ♀, Surinam.

*Callimormus juventus* Scudder, 1872. — Evans (1955). RMNH: 1 ♂, 1 ♀, Kwatta, Lelydorp.

*Callimormus corades* Felder, 1862. — Williams & Bell (1931). RMNH: 4 ♂, 1 ♀, Domburg, Lelydorp, Paramaribo, Zorg en Hoop.

*Callimormus saturnus* Herrich-Schäffer, 1869. — Evans (1955). ITZ: 2 ♀, Paramaribo.

RMNH: 2 ♂, 1 ♀, Ma Retraite, Zorg en Hoop.

*Eutocus facilis* Plötz, 1884. — Plötz (1884).

*Eutocus fabulinus* Plötz, 1884. — Plötz (1884).

*Eutocus matildae vinda* Evans, 1855. — RMNH: 3 ♂, Avanavero Vallen, Ma Retraite, Surinam.

*Virga virginius* Möschler, 1882. — Möschler (1882).

*Methionopsis ina* Plötz, 1882. — Evans (1955). RMNH: 2 ♂, 3 ♀, Domburg, Ma Retraite, Paramaribo.

*Sodalia sodalis* Butler, 1877. — Evans (1955); Williams & Bell (1931, "Euroto saramacca"). RMNH: 3 ♂, 3 ♀, Ma Retraite, Paramaribo.

*Mnestheus servilius* Möschler, 1882. — Möschler (1882).

*Artines aepitus* Geyer, 1832. — Williams & Bell (1931, "Artines atizies Godman"). RMNH: 1 ♂, 1 ♀, Goliath Kreek, Surinam. ZSM: 2 ♂, 1 ♀, Surinam.

*Aecas aecas* Stoll, 1781. — Stoll (1781); Williams & Bell (1931). RMNH: 2 ♂, 4 ♀, Domburg, Ma Retraite, Surinam, Zanderij. ZSM: 1 ♂, Surinam.

*Mnaseas bicolor* Mabille, 1889. — Williams & Bell (1931).

*Thargella caura* Plötz, 1882. — Möschler (1882); Plötz (1882b); Williams & Bell (1931, "Thargella fuliginosa Godman"). RMNH: 2 ♂, Domburg.

*Venas evans* Butler, 1877. — RMNH: 1 ♂, Lely Gebergte. ZSM: 9 ♂, 2 ♀, Surinam.

*Venas caerulans* Mabille, 1878. — ZSM: 1 ♂, Surinam.

*Monca telata* Herrich-Schäffer, 1869. — Möschler (1882).

*Nastraea chao* Mabille, 1897. — Williams & Bell (1931, "Megistias huascari Lindsey"). It is not certain, if the name given by Lindsey is really a synonym of Mabille's name.

*Nastraea guianae* Lindsey, 1925. — RMNH: 5 ♂, 4 ♀, Charlesburg, Paramaribo, Zanderij, Zorg en Hoop. See Note 23.

*Cymaenes tripunctus theogenis* Capronnier, 1874. — Evans (1955); Möschler (1882, "Pamphila ancus"); Williams & Bell (1931). RMNH: 2 ♂, 6 ♀, Charlesburg, Kwatta, Lelydorp, Ma Retraite.

*Cymaenes geijskesi* spec. nov. — See Note 21.

*Cymaenes tripunctata alumna* Butler, 1877. — Evans (1955); Möschler (1882, "Pamphila obsoleta"); Williams & Bell (1931). NZC: 1 ♀, Manlobbi. RMNH: 1 ♂, 2 ♀, Charlesburg, Domburg, Paramaribo.

- Vehilius stictomenes stictomenes* Butler, 1877. — Evans (1955); Möschler (1882, "Apautus venosus Pittw."); Williams & Bell (1931, "Vehilius venosus Plötz"). NZC: 1 ♂, Paramaribo. RMNH: 5 ♂, 7 ♀, Avanavero Vallen, Domburg, Lelydorp, Ma Retraite, Paramaribo, Zanderij. ZSM: 2 ♂, Surinam.
- Vehilius inca* Scudder, 1872. — Evans (1955); Williams & Bell (1931, "Megistias labdacus Godman"). NZC: 1 ♂, Paramaribo. RMNH: 7 ♂, 2 ♀, Domburg, Kwatta, Lelydorp, Ma Retraite, Paramaribo, Zorg en Hoop.
- Vehilius almoneus* Schaus, 1902. — ITZ: 1 ♀, Paramaribo. RMNH: 5 ♂, 6 ♀, Charlesburg, Domburg, Kwatta, Paramaribo.
- Vehilius major* spec. nov. — See note 22.
- Vehilius vetulus* Mabille, 1878. — Evans (1955). RMNH: 2 ♂, Brownsberg, Lely Geberge.
- Vehilius seriatus* seriatus Mabille, 1891. — RMNH: 1 ♂, Coeroeni Eiland. (= *Vehilius vetustus* Mielke, 1968, nomen novum pro *Cobalus vetulus* Mabille, 1883).
- Mnasilus allubita* Butler, 1877. — Williams & Bell (1931, "Mnasilus penicillatus Godman"). ITZ: 1 ♂, Paramaribo. RMNH: 9 ♂, 4 ♀, Charlesburg, Lelydorp, Ma Retraite, Paramaribo, Zanderij, Zorg en Hoop. ZSM: 1 ♂, Surinam. See Note 23.
- Mnasitheus simplicissima* Herrich-Schäffer, 1870. — Williams & Bell (1931).
- Mnasitheus similis* spec. nov. — See Note 24.
- Moeris remus* Fabricius, 1798. — Evans (1955); Williams & Bell (1931).
- Parphorus storax* Mabille, 1891. — Williams & Bell (1931). RMHN: 2 ♂, Brokopondo, Lawa.
- Parphorus decora* Herrich-Schäffer, 1869. — Williams & Bell (1931), "Phlebodes fartuga Schaus". RMNH: 2 ♂, Makambi-kreek, Ma Retraite. ZSM: 1 ♂, Surinam.
- Papias phainis* Godman, 1900. — RMNH: 1 ♀, Brownsberg. See Note 25.
- Papias phaeomelas* Geyer, 1831. — Möschler (1882); Williams & Bell (1931). RMHN: 2 ♂, 1 ♀, Brownsberg, Domburg.
- Papias subcostulata integra* Mabille, 1891. — Evans (1955). NZC: 1 ♂, Republiek. RMNH: 3 ♂, Brokopondo, Brownsberg, Domburg.
- Papias proximus* Bell, 1934. — RMNH: 1 ♂ Sipaliwini.
- Cobalopsis venias* Bell, 1942. — RMNH: 1 ♂, Copi.
- Cobalopsis dorpa* spec. nov. — See Note 26.
- Cobalopsis tanna* spec. nov. — See Note 27.
- Cobalopsis catocala* Herrich-Schäffer, 1869. — Williams & Bell (1931).
- Lerema ancillaris* Butler, 1877. — Plötz (1886, "Hesperia mulla"). RMNH: 7 ♂, 4 ♀, Charlesburg, Domburg, Kwatta, Ma Retraite, Paramaribo, Zanderij, Zorg en Hoop.
- Morys compta* compta Butler, 1877. — Evans (1955); Plötz (1886, "Hesperia aethra"); Williams & Bell (1931, "Euroto compta" and "Euroto micythus Cramer").
- Morys geisa* geisa Möschler, 1978. — Evans (1955). RMNH: 4 ♂, 1 ♀, Lelydorp, Ma Retraite, Paramaribo.
- Morys subgrisea* *paradoxa* subspec. nov. — See Note 28.
- Vettius lafresnayei* pica Herrich-Schäffer, 1869. — RMNH: 2 ♂, 1 ♀, Brownsberg, Sipaliwini.
- Vettius richardi* Weeks, 1906. — RMNH: 1 ♂, 1 ♀, Berlijn, Brokopondo.
- Vettius triangularis* Geyer, 1831. — Williams & Bell (1931). ZSM: 1 ♀, Surinam.
- Vettius monacha* Plötz, 1882. — Evans (1955); Möschler (1882). ZSM: 1 ♂, 1 ♀, Surinam.
- Vettius phyllus* phyllus Cramer, 1777. — Cramer (1777); Evans (1955); Williams & Bell (1931, "Vettius laurea Hewitson"). RMNH: 1 ♂, 1 ♀, Blakawatra. ZSM: 1 ♂, Surinam.
- Vettius marcus* Fabricius, 1787. — Evans (1955); Williams & Bell (1931).
- Vettius fantasos* fantasos Stoll, 1780. — Plötz (1882b, "Hesperia eucherus"); Sepp (1847); Stoll (1780); Williams & Bell (1931). RMNH: 2 ♂, 2 ♀, Blakawatra, Domburg.
- Vettius artona* Hewitson, 1868. — Evans (1955); Williams & Bell (1931). RMNH: 1 ♀, Zanderij-Phedra.
- Vettius yalta* Evans, 1955. — RMNH: 2 ♀, Coeroeni Eiland, Paramaribo. See Note 29.
- Vettius tertianus* Herrich-Schäffer, 1869. — Möschler (1882 "Pamphila warra" and "Pamphila zola").
- Paracarystus hypargyra* Herrich-Schäffer, 1869. — Evans (1955); Möschler (1876; 1882, record of 1876 was false). RMNH: 3 ♂, Domburg, Paramaribo, Surinam.
- Paracarystus menestriesi rona* Hewitson, 1866. — Evans (1955). RMNH: 2 ♂, 1 ♀, Brownsberg, Phedra. ZSM: 2 ♂, Surinam.
- Turesis lucas* Frabricius, 1793. — Möschler (1876). RMNH: 3 ♂, 1 ♀, Domburg.
- Thoön dubia* Bell, 1932. — RMNH: 2 ♂, 1 ♀,

- Brownsberg, Patamakka Rivier.
- Thoon taxes* Godman, 1900. — RMNH: 1 ♂,  
Ma Retraite.
- Justinia phaetusa phaetusa* Hewitson, 1866. —  
RMNH: 4 ♂, 1 ♀, Lely Gebergte, Phedra,  
Rama.
- Justinia gava* Evans, 1955. — Evans (1955).
- Justinia justinianus dappa* Evans, 1955. — Wil-  
liams & Bell (1931, "Eutychide cingulicornis  
Herrich-Schäffer").
- Eutychide complana* Herrich-Schäffer, 1869. —  
Evans (1955); Williams & Bell (1931).  
RMNH: 2 ♀, Albina, Surinam.
- Eutychide subcordata subcordata* Herrich-  
Schäffer, 1869. — Evans (1955). RMNH: 1  
♂, 1 ♀, Republiek, Sipaliwini.
- Eutychide subpunctata intermedia* subspec. nov.  
— See Note 30.
- Onophas columbaria columbaria* Herrich-  
Schäffer, 1870. — Evans (1955).
- Naevolus orius orius* Mabille, 1883. — RMNH:  
2 ♂, 2 ♀, Goliath Kreek, Paramaribo, Zan-  
derij.
- Enosis angularis* Möschler, 1876. — Möschler  
(1876; 1882, "Proteides parvipuncta" and  
"Carystus infuscatus Plötz"). RMNH: 6 ♂,  
3 ♀, Albina, Leonsberg, Paramaribo, Surinam.
- Vertica verticalis grandipuncta* Mabille, 1883. —  
RMNH: 2 ♀, Blakawatra, Ma Retraite.
- Ebusus ebusus* Stoll, 1780. — Evans (1955);  
Möschler (1876, "Carystus psecas Cr.");  
Stoll (1780; 1781, "Papilio psecas"). RMNH:  
1 ♂, 3 ♀, Rama, Surinam, Zanderij. ZSM: 3  
♂, 2 ♀, Surinam.
- Talides sergestus* Cramer, 1775. — Cramer  
(1775); Möschler (1876); Williams & Bell  
(1931). RMNH: 2 ♂, 1 ♀, Paramaribo, Zan-  
derij.
- Talides sinois sinois* Hübner, 1819. — Evans  
(1955); Hübner (1819); Stoll (1781, "Papilio  
sinon"). RMNH: 2 ♂, 1 ♀, Domburg, Para-  
maribo, Surinam. See Note 31.
- Talides alternata alternata* Bell, 1941. — Evans  
(1955). RMNH: 2 ♂, Paramaribo. See Note  
31.
- Nyctus biarbas* Cramer, 1775. — Cramer  
(1775).
- Carystus elvira* Plötz, 1882. — RMNH: 1 ♀,  
Surinam. See Note 32.
- Carystus hocus* Evans (1955). — Evans (1955).  
NZC: 1 ♂, Grangoela.
- Carystus jolus* Stoll, 1782. — Evans (1955); Stoll  
(1782). RMNH: 1 ♀, Saramacca Rivier.
- Carystus senex* Plötz, 1882. — ITZ: 1 ♂, 1 ♀,  
Paramaribo. RMNH: 1 ♀, Paramaribo.
- Carystus junior* Evans, 1955. — RMNH: 2 ♂, 3  
♀, Charlesburg, Lelydorp, Mariënburg,  
Powakka, Surinam.
- Carystus phorcus phorcus* Cramer, 1777. —  
Cramer (1777); Evans (1955); Möschler  
(1882, "Carystus claudianus Ltrll." and  
"Proteides marpesia Hew."). ITZ: 2 ♀, Par-  
amaribo. RMNH: 3 ♀, Paramaribo. ZSM: 1  
♀, Surinam.
- Telles arcalaus* Stoll, 1782. — Sepp (1850, "Pa-  
pilio uraniae"); Stoll (1782). RMNH: 1 ♀,  
Surinam.
- Moeros moeros* Möschler, 1876. — Evans  
(1955); Möschler (1876). RMNH: 1 ♂, 2 ♀,  
Paramaribo; agreeing with description and  
figures, but midtibiae spined (cf. Evans,  
1955: 239).
- Cobalus virbius virbius* Cramer, 1777. —  
Cramer (1777); Evans (1955); Möschler  
(1876); Williams & Bell (1931). ITZ: 1 ♀,  
Paramaribo. ZSM: 5 ♂, Surinam.
- Cobalus calvina* Hewitson, 1866. — RMNH: 1  
♂, Zanderij. ZSM: 9 ♂, Surinam.
- Dubiella fiscella* Hewitson, 1877. — Williams &  
Bell (1931).
- Dubiella dubius* Stoll, 1781. — Stoll (1781).  
RMNH: 3 ♂, 1 ♀, Moengotapoe-Wia-Wia.
- Tellona variegata* Hewitson, 1870. — Bell  
(1931, "Thracides currani"). RMNH: 1 ♂, 2  
♀, Brownsberg.
- Damas clavus* Herrich-Schäffer, 1869. — Evans  
(1955); Möschler (1876, "Proteides cervus").  
RMNH: 3 ♂, Patamakka Rivier, Zanderij.  
ZSM: 4 ♂, 1 ♀, Surinam.
- Orphe gerasa* Hewitson, 1871. — RMNH: 1 ♂,  
Surinam.
- Carystoides basoches basoches* Latreille, 1824.  
— Evans (1955); Möschler (1876, "Proteides  
brinoides" and "Caristus basochesii Ltrll.");  
Williams & Bell (1931). ITZ: 1 ♀, Surinam.  
RMNH: 4 ♂, 2 ♀, Paramaribo, Surinam,  
Zanderij. ZSM: 2 ♂, 1 ♀, Surinam (♀ possi-  
bly type of *Proteides brinoides* Möschler).  
See Note 32.
- Carystoides noseda* Hewitson, 1866. — Evans  
(1955). NZC: 1 ♂, Lelydorp. See Note 33.
- Carystoides sicania orbis* Godman, 1901. —  
Evans (1955). RMNH: 3 ♂, Coeroeni Eiland,  
Linker Coppename Rivier, Patamakka.  
ZSM: 1 ♂, Surinam.
- Carystoides maroma* Möschler, 1876. — Evans  
(1955); Möschler (1876); Plötz (1882b,

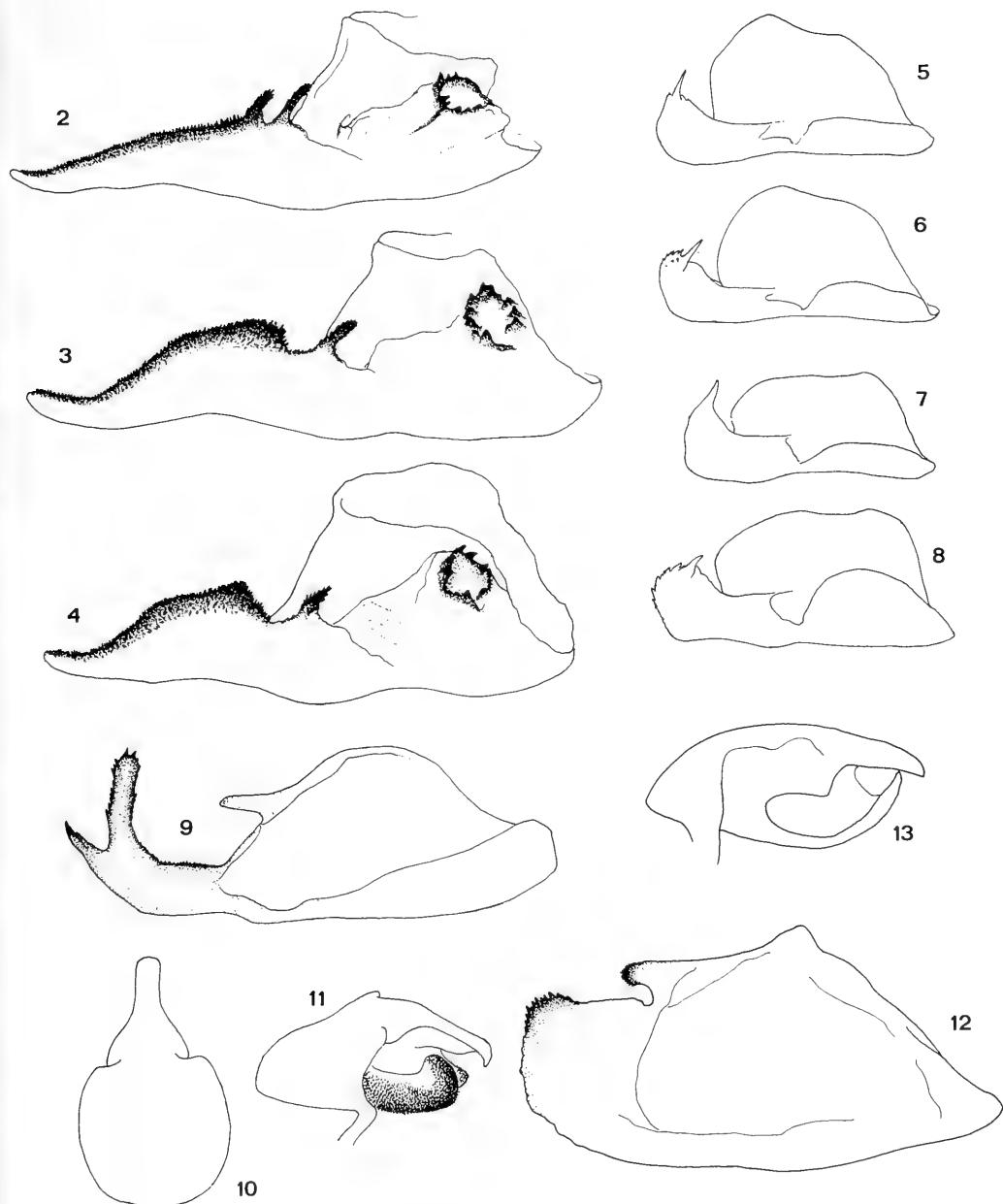
- "*Hesperia valentina*").
- Carystoides cathaea* Hewitson, 1866. — Evans (1955).
- Perichares butus* Möschler, 1876. — Möschler (1876). RMNH: 2 ♂, Domburg, Surinam.
- Perichares philetis philetis* Gmelin, 1790. — Evans (1955); Möschler (1876), "Caristus corydon Fb."); Williams & Bell (1931, "Perichares [sic!] coridon Fabricius"). RMNH: 4 ♂, 6 ♀, Domburg, Lelydorp, Paramaribo, Surinam. ZSM: 1 ♂, Surinam.
- Perichares lotus* Butler, 1870. — Williams & Bell (1931). RMNH: 1 ♂, Domburg.
- Perichares deceptus* Butler & Druce, 1872. — RMNH: 1 ♂, Rama. See Note 34.
- Orses cynisca* Swainson, 1821. — RMNH: 1 ♂, Gansee.
- Lycas godarti boisduvalii* Ehrmann, 1909. — Möschler (1876, "Proteides ceraca Hew."). RMNH: 1 ♂, Domburg.
- Saturnus tiberius* Möschler, 1882. — Möschler (1882); Williams & Bell (1931, "Phlebodes tiberius Möschler" and "Phlebodes reticulata Plötz").
- Phlebodes pertinax* Stoll, 1781. — Evans (1955); Stoll (1781). RMNH: 1 ♂, Zanderij-Phedra.
- Phlebodes meesi* spec. nov. — See Note 35.
- Joanna boxi* Evans, 1955. — RMNH: 1 ♂, Surinam.
- Quinta cannae* Herrich-Schäffer, 1869. — Evans (1955); Möschler (1882, "Proteides osembo"). ITZ: 1 ♂, Paramaribo. RMNH: 3 ♂, 4 ♀, Ma Retraite, Paramaribo.
- Cyne'a anthracinus luctatius* Schaus, 1913. — RMNH: 1 ♂, 1 ♀, Brownsberg, Domburg.
- Cyne'a cyrus* Plötz, 1883. — RMNH: 2 ♂, Rama. See Note 36.
- Cyne'a iquita* Bell, 1941. — Evans (1955).
- Cyne'a corisana* Möschler, 1882. — Möschler (1882).
- Cyne'a diluta* Herrich-Schäffer, 1869. — Evans (1955); Möschler (1882, "Pamphila zeppa"); Plötz (1883, "Hesperia vellejus"); Williams & Bell (1931, "Cobalus zeppa Möschler"). ITZ: 1 ♀, Surinam. RMNH: 3 ♂, 1 ♀, Domburg, Ma Retraite, Paramaribo.
- Cyne'a corope* Herrich-Schäffer, 1869. — Möschler (1882).
- Penicula bryanti* Weeks, 1906. — Evans (1955). RMNH: 6 ♂, Domburg, Ma Retraite.
- Penicula criska extrema* subsp. nov. — See Note 37.
- Decinea lucifer* Hübner, 1831. — Hübner (1831).
- Conga chydaea* Butler, 1870. — Williams & Bell (1931, "Prene's vala Mabilie").
- Hylephila phyleus phyleus* Drury, 1773 (for correct spelling, see Brown & Heineman, 1972: 408). — Williams & Bell (1931). ITZ: 6 ♂, 1 ♀, Paramaribo. RMNH: 9 ♂, 4 ♀, Brokoppo, Ma Retraite, Matapi, Paramaribo, Zanderij, Zorg en Hoop.
- Hesperia uncas* Edwards, 1863. — Möschler (1882, 2 ♂ from Paramaribo, identified as *Hesperia uncas* by Plötz); identification or locality labels false, the species is North American.
- Polites vibex* Geyer, 1832. — Williams & Bell (1931). ITZ: 4 ♂, Paramaribo, Zanderij. NZC: 1 ♀, Paramaribo. RMNH: 8 ♂, 2 ♀, Domburg, Paramaribo, Surinam. See Note 38.
- Polites vibicoides* spec. nov. — See Note 39.
- Polites coras* Cramer, 1775. — Cramer (1775); Williams & Bell (1931, "Catia otho Smith & Abbot"). A purely North American species. The locality of Cramer's type must have been false. The observation of Williams & Bell must be based on a misidentification.
- Wallengrenia druryi curassavica* Snellen, 1887. — Evans (1955); Möschler (1882). RMNH: 12 ♂, 15 ♀, Albina, Domburg, Ma Retraite, Paramaribo, Raleigh Vallen, Rama, Surinam.
- Wallengrenia premnas* Wallengren, 1860. — Evans (1955).
- Pompeius pompeius* Latreille, 1824. — Evans (1955); Möschler (1882); Williams & Bell (1931, "Polites athenion Hübner"). ITZ: 15 ♂, 10 ♀, Charlesburg, Leiding, Paramaribo, Republiek, Zanderij. NZC: 1 ♀, Paramaribo. RMNH: 23 ♂, 12 ♀, Albina, Brokopondo, Brownsberg, Charlesburg, Coeroeni Eiland, Domburg, Lelydorp, Ma Retraite, Paramaribo, Surinam.
- Choranthus vitellius* Fabricius, 1793. — Williams & Bell (1931).
- Mellana clavus* Erichson, 1848. — Williams & Bell (1931, "Atrytone mella Godman" and "Atrytone barbara").
- Mellana helva* Möschler, 1876. — Möschler (1876).
- Mellana villa* Evans, 1955. — RMNH: 1 ♂, 4 ♀, Brownsberg, Ma Retraite, Paramaribo, Surinam.
- Euphyes sirene kayei* Bell, 1931. — Evans (1955). RMNH: 1 ♂, Zanderij.
- Metron chrysogastra chrysogastra* Butler, 1870. — RMNH: 1 ♂, Sipaliwini.

- Metron fasciata* Möschler, 1876. — Möschler (1876). RMNH: 3 ♂, Domburg, Ma Retraite.
- Propertius phineus* Cramer, 1777. — Cramer (1777); Evans (1955, "Propertius albistriga Tessmann"). RMNH: 1 ♂, Surinam, holotype. See De Jong (1983).
- Calpodes ethlius* Stoll, 1782. — Evans (1955); Stoll (1782). ITZ: 1 ♂, Paramaribo. RMNH: 5 ♂, 6 ♀, Ma Retraite, Paramaribo, Powaka, Zanderij.
- Panoquina panoquinoides minima* subsp. nov. — See Note 40.
- Panoquina ocola* Edwards, 1863. — Evans (1955); Möschler (1882, "Pamphila ortygia"). ITZ: 11 ♂, 8 ♀, Charlesburg, Leiding, Paramaribo, Republiek. NZC: 1 ♂, Republiek. RMNH: 4 ♂, 2 ♀, Coppename Rivier, Ma Retraite, Morico Kreek, Paramaribo, Republiek.
- Panoquina sylvicola* Herrich-Schäffer, 1865. — Evans (1955); Möschler (1876). RMNH: 4 ♂, 5 ♀, Brownsberg, Carolina Kreek, Lelydorp, Ma Retraite, Paramaribo.
- Panoquina fusina fusina* Hewitson, 1868. — Evans (1955); Williams & Bell (1931). RMNH: 4 ♂, Charlesburg, Morico Kreek, Paramaribo.
- Panoquina evadnes* Stoll, 1781. — Evans (1955); Plötz (1882, "Hesperia chlorus"). RMNH: 5 ♂, 4 ♀, Paramaribo, Surinam.
- Nyctelius nyctelius* Latreille, 1824. — Evans (1955); Williams & Bell (1931). RMNH: 1 ♂, 2 ♀, Lelydorp, Paramaribo, Surinam.
- Thespies dalman* Latreille, 1824. — Evans (1955).
- Vacerra bonfilii litana* Hewitson, 1866. — Williams & Bell (1931).
- Oxynthes corusca* Herrich-Schäffer, 1869. — ZSM: 1 ♀, Surinam.
- Niconiades yoka* Evans, 1955. — RMNH: 1 ♂, 1 ♀, Morico Kreek, Patamakka Rivier.
- Niconiades nikko* Hayward, 1948. — NZC: 1 ♂, Ma Retraite. RMNH: 5 ♂, 1 ♀, Ma Retraite, Paramaribo.
- Niconiades caeso* Mabille, 1891. — Williams & Bell (1931); possibly misidentification, southern species only known from Paraguay and S. Brazil.
- Aides epitius epitius* Stoll, 1781. — Evans (1955); Stoll (1781). RMNH: 1 ♂, Zanderij.
- Aides brino* Stoll, 1781. — Stoll (1781).
- Aides aegita* Hewitson, 1866. — RMNH: 2 ♂, 4 ♀, Paramaribo, Surinam.
- Aides ocrinus* Plötz, 1882. — Möschler (1882).
- Xeniades chalestra* Hewitson, 1866. — RMNH: 1 ♂, 2 ♀, Paramaribo, Surinam.
- Xeniades orchamus* Cramer, 1777. — Cramer (1777). RMNH: 2 ♂, 6 ♀, Paramaribo, Surinam (including ♀ holotype, Surinam).
- Cravera rara* gen. nov. et spec. nov. — See Note 41.
- Surina unica* gen. nov. et spec. nov. — See Note 42.
- Saliana chiomara* Hewitson, 1871. — Evans (1955). RMNH: 1 ♀, Paramaribo.
- Saliana fischeri* Latreille, 1824. — Evans (1955). RMNH: 1 ♂, Surinam.
- Saliana nigra* Evans, 1955. — Evans (1955).
- Saliana esperi* Evans, 1955. — Evans (1955). ZSM: 4 ♂, Surinam.
- Saliana antoninus* Latreille, 1824. — Evans (1955); Möschler (1876). ITZ: 1 ♀, Paramaribo. RMNH: 3 ♂, 3 ♀, Brownsberg, Ma Retraite, Surinam, Zanderij.
- Saliana longirostris* Sepp, [1840]. — Evans (1955); Sepp (1832—1840). RMNH: 3 ♂, 3 ♀, Albina, Domburg, Ma Retraite, Paramaribo, Patamakka Rivier. ZSM: 1 ♂, 1 ♀, Surinam.
- Saliana morsa* Evans, 1955. — Evans (1955). RMNH: 1 ♂, Zanderij.
- Saliana salius* Cramer, 1775. — Cramer (1775); Evans (1955); Möschler (1876, "Thracides telegonus Esper"); Williams & Bell (1931, "Thracides telegonus Esper"). ITZ: 1 ♀, Paramaribo. NZC: 1 ♂, Republiek. ZSM: 4 ♂, Surinam.
- Thracides phidon* Cramer, 1779. — Cramer (1779); Evans (1955); Möschler (1876); Sepp (1841, "Papilio pyrophorus"). RMNH: 2 ♂, Charlesburg, Paramaribo.
- Neoxeniades cincia* Hewitson, 1871. — RMNH: 1 ♂, 1 ♀, Goliath Kreek. See Note 43.
- Neoxeniades braesia* Hewitson, 1867. — RMNH: 1 ♀, Goliath Kreek. See Note 44.
- Pyrrhopygopsis socrates orasus* Druce, 1876. — RMNH: 1 ♂, 1 ♀, Batavia, Surinam.

## NOTES ON THE HESPERIIDAE OF SURINAM

1. *Pyrrhopyge phidias* Linnaeus, 1758.

Evans (1951) recognized 10 subspecies. They are, however, not geographically defined, several subspecies being sympatric. For Surinam, for instance, the following "subspecies" are recorded: *bixae* Linnaeus, *garata* Hewitson, and *phidias* Linnaeus. Among the specimens from Surinam in RMNH there are, moreover, two



Figs. 2—4. *Elbella* species, inside of left valva; 2, *E. bicuspis* spec. nov., Paramaribo (Surinam); 3, *E. umbrata acala*, Muzo (Colombia); 4, *E. umbrata umbrata*, Rio Pancartambo (Peru). Figs. 5—8, *Urbanus* species, inside of left valva; 5, *U. ambiguus* spec. nov., Surinam; 6, *U. teleius*, Domburg (Surinam); 7, *U. simplicius*, Avanavero Vallen (Surinam); 8, *U. zagorus*, Surinam. Figs. 9—11, *Bungalotis sipa* spec. nov. Sipaliwini (Surinam); 9, inside of left valva; 10, dorsal view of tegumen and uncus; 11, lateral view of tegumen, uncus and gnathos. Figs. 12—13, *Clito jonkersi* spec. nov., Domburg (Surinam); 12, inside of left valva; 13, lateral view of tegumen, uncus and gnathos. Figs. 2—11 drawn at same magnification, 12—13 at twice this magnification.

males agreeing with "subspecies" *zenodorus* Godman & Salvini. Apparently the subspecific classification of this species does not correctly reflect the pattern of variation. In this case it is better to abandon the subspecies at all and to describe the variation in a more appropriate way. The possibility of more than one species being involved cannot be ruled out.

### 2. *Pyrrhopage charybdis* Westwood, 1852.

The single male from Surinam in RMNH has a forewing length of 26.4 mm, a dark indigo blue shine and veins not conspicuously black. It thus agrees with ssp. *semita* Evans, 1951, the southernmost of the two subspecies recognized by Evans for this essentially central and southern Brazilian species. A male in RMNH with identical genitalia and same colouring from Porto Alegro, has a forewing length of 24 mm, and comes close to ssp. *charybdis* Westwood, as far as size is concerned. As the distribution areas of the two subspecies defined by Evans (1951) partly overlap, the recognition of two subspecies is doubtful.

### 3. *Pyrrhopage cometes* Cramer, 1779.

The single male from Surinam in RMNH has size and spots as in Peruvian specimens (ssp. *staudingeri* Plötz, 1879) and is unlike a male from French Guiana in RMNH (ssp. *cometes*) (cf. Evans, 1951: 35). Either the locality is false, or the variation is more complicated than suggested by the subspecific classification by Evans (1951), as is often the case in *Pyrrhopage* species.

### 4. *Elbella bicuspis* spec. nov.

External characters (figs. 49, 50). — Belonging to *patrobas* group of species (Evans, 1951: 42): *Jemadia*-like, forewing spot in space 3 free, spot in space 4 in line with those in 5—7. Forewing, no spot in space 9, a tiny one in space 10 far basad of the spot in space 8. Hyaline spot in space 1b narrow, pointed, not entirely reaching middle of space 1b. Blue subbasal bar on upper side at almost right angles to dorsum, not parallel with central hyaline band. Hindwing upper side, blue bands not extending beyond vein 7. Hindwing underside, subbasal blue band from space 8 across cell to vein 1b, directed to midway dorsum; central blue band as wide as dark area between it and subbasal band, directed to dorsum above tornus; inner discal band from vein 8 tapering to vein 3, narrow in spaces 3 and 4/5; outer discal band from vein 6 to vein 1b;

blue submarginal scaling inconspicuous, close to outer discal band; a narrow blue bar in space 7 between central and inner discal bands. Length of forewing, 24.2 mm.

Male genitalia (figs. 2—4). — Very much like *Elbella umbrata* Mabille & Bouillet, 1908, but cucullus slenderer, straighter, and with two dorsal prongs instead of one (hence the name of the species).

Identification. — As remarked by Evans (1951: 42) the species of the *patrobas* group can only be determined with certainty by genitalia examination. The present species, however, differs from all other species of the group in the blue subbasal bands on the upper side of the forewing and underside of the hindwing being clearly less oblique. In all other species of the group the subbasal and central bands on the underside of the hindwing generally point to the tornus, while in the new species they point to the dorsum above the tornus.

Material examined. — Holotype, ♂, Paramaribo, leg. E. H. Jonkers (RMNH).

### 5. *Jemadia fallax fallax* Mabille, 1878.

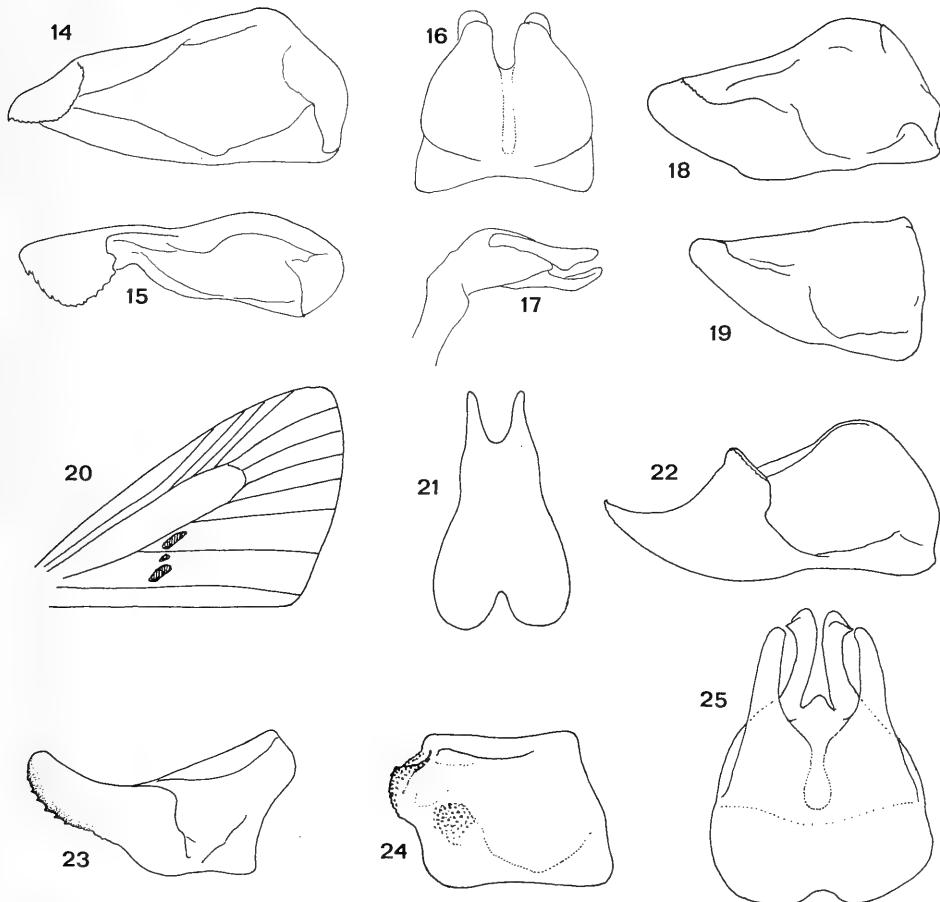
The four males from Surinam in RMNH show some variation in the serration of the cucullus, and are strikingly different in the shape of the cucullus, which varies from semicircular to ovate. There is no reason to consider it otherwise than individual variation.

### 6. *Phocides pigmalion hewitsonius* Mabille, 1883.

Hyaline spots of forewing hardly, if at all different from those in males from Honduras and Colombia (ssp. *pigmalion* Cramer, 1779), but on upper side of hindwing blue postdiscal band reduced, especially in spaces 4/5 and 6. Therefore, the original figure of "*Papilio pigmalion*" by Cramer (1779: fig. 245a) differs from specimens from Surinam, and as correctly suggested by Evans (1952: 13), Cramer's figure must represent a specimen that did not come from Surinam.

### 7. *Entheus gentius* Cramer, 1779.

In the females, there is much variation in the position of the hyaline spots of the forewing. The upper spot in space 1b and the spot in space 2 are always conjoined, but the position of the spot in space 2 varies relative to the cell spot from being completely in line to widely separate, so that the spot in space 2 is midway between the spot in space 3 and the cell spot. In



Figs. 14—17. *Cymaenes geijskesi* spec. nov., Zanderij (Surinam); 14, inside of left valva; 15, dorsal view of left valva; 16, dorsal view of tegumen and uncus; 17, lateral view of tegumen, uncus and gnathos. Fig. 18, *Vehilius major* spec. nov., Patamakka Rivier (Surinam), inside of left valva. Fig. 19, *Vehilius vetula*, Brownsberg (Surinam), inside of left valva. Figs. 20—22, *Mnasitheus similis* spec. nov., Surinam; 20, ♂ forewing venation and brands (hatched); 21, dorsal view of tegumen and uncus; 22, inside of left valva. Fig. 23, *Cobalopsis dorpa* spec. nov., Paramaribo (Surinam), inside of left valva. Figs. 24—25, *Cobalopsis tanna* spec. nov., Domburg (Surinam); 24, inside of left valva; 25, dorsal view of tegumen and uncus. All parts of genitalia drawn at same magnification.

addition there is much variation in the number and length of the processes on either side of the ostium bursae. The variation in the markings as well as in the genitalia seems to be continuous.

#### 8. *Aguna claxon* Evans, 1952.

The genitalia and external characters agree well with this species, but the spot in space 3 of the forewing is at least as far from the spot in space 2 as its own width and not overlapping as stated by Evans (1952: 60) in the original description.

#### 9. *Polythrix asine* Hewitson, 1867.

The single female from Surinam in RMNH agrees well with this species, but on the upper side of the forewing the inner edge of the spot in space 2 is not in line with the inner edge of the cell spot, being at a right angle with vein 2. As the female genitalia of *Polythrix* species are practically unknown, the identification must remain provisionally for the time being.

#### 10. *Polythrix caunus* Herrich-Schäffer, 1869.

The male genitalia agree completely with

those of *P. caunus*, but contrary to what is stated by Evans (1952: 71), the spot in space 9 of the forewing is absent in two males and only a tiny dot in the other males. Moreover, on the forewing there is a well-developed spot in space 1b under the outer part of the spot in space 2 in both females, and a tiny dot in the same place in two males. Consequently, without the help of the genitalia it is impossible to identify these specimens with Evans' key.

#### 11. *Urbanus esma* Evans, 1952.

The dorsal process of the cucullus is distinctly shorter and stouter than in *U. esmeraldus* Butler, as stated by Evans (1952: 90), but the outline of the valve seems to be similar in both species, contrary to Evans' very schematic drawings.

#### 12. *Urbanus ambiguus* spec. nov.

External characters (figs. 51, 52). — Male, length of forewing 21 mm. No costal fold. Upperside uniformly brown, including head, body and wing bases. Fringes brown, unchequered. Forewing with a narrow central hyaline band from middle of space 1b to costa, composed of upper spot in space 1b, spots in spaces 2, 3, and cell, and two small spots over cell spot. Inconspicuous linear spots in spaces 4 and 5, the latter more or less in line with the subequal spots in spaces 6 to 9. On underside of hindwing central band connected to outer spot in space 7, widening towards vein 1b; discal band from vein 7 to vein 1b, with irregular sides, widening towards vein 1b and here almost touching the central band.

Male genitalia (figs. 5—8). — Costa bulging so that total height of valve is twice height of cucullus (without spine). Cucullus with a strong apical spine and a few inconspicuous short spines.

Identification. — The species falls within what can be called the *teleus* group of species, characterized by the uniformly brown upper side with unchequered brownish fringes and spot in space 3 forming part of the central band. By the absence of a costal fold and the conjoined cell spot and outer spot in space 7 on the underside of the hindwing, the species keys to *U. cindra* Evans with Evans (1952). It differs, however, from this species in the presence of spots in spaces 4 and 5 and a well-developed spot in space 9 of the forewing, and in the bulging costa of the valve. In the latter character it is similar to *U. teleus* Hübner, which, however, is

more strongly spined in the apical part of the cucullus and has, moreover, the cell spot on the underside of the hindwing central between the inner and outer spots in space 7. In figs. 6—8 the valves of some related species are given for comparison.

Material examined. — Holotype, ♂, Surinam (RMNH).

#### 13. *Astraptes cretatus* Hayward, 1939.

In the male the white tornal area on the underside of the forewing extends up to the cell, in the female it enters the cell almost up to the radius. Costa of forewing on underside hardly with any white. By these characters the specimens are intermediate between spp. *cretatus* and spp. *adoba* Evans, 1952.

#### 14. *Bungalotis sipa* spec. nov.

External characters (figs. 53, 54). — Male, length of forewing 22.6 mm. Ground colour upper side orange-brown, dark brown in spaces 7 and 8 of hindwing. Forewing with narrow but conspicuous dark markings in spaces 1b, 2, 3, and 4 to 8, the latter in a curved line, and a dark bar across the cell just before the origin of vein 3; spot in space 2 midway between the origin of vein 3 and the spot in space 3, far from the cell spot. Hindwing with an irregular series of dark spots in spaces 1b to 6 and a dark spot at end cell. Underside similar, with broad dark suffusion along termen of forewing and along costa and termen of hindwing, and light ochreous along dorsum of forewing up to middle of space 1b. Spots in spaces 1b and 2 on underside of forewing with whitish scales in centre, similarly on underside of hindwing discal spots in spaces 1c to 7 (in space 1c a double spot), basal spot in space 1c, and spot at end cell; subbasal spot in space 7 without whitish scales.

Male genitalia (figs. 9—11). — Uncus relatively long and narrow, 1.3 times as long as greatest width, more than 4 times as long as at narrowest point. Cucullus bifurcate apically, lower arm slightly serrate and pointed, upper arm much larger, irregularly serrate, dorsal edge of cucullus finely serrate.

Identification. — By the position of the spots on the upper side of the hindwing the specimen keys to *B. quadratum* Sepp (cf. Evans, 1952: 140), but the latter is a larger insect (male forewing length 26 mm), with a lighter, yellowish tinge and less conspicuous, broader spots. The narrow uncus and general shape of the valve are suggestive of *B. borax lactos* Evans, which is

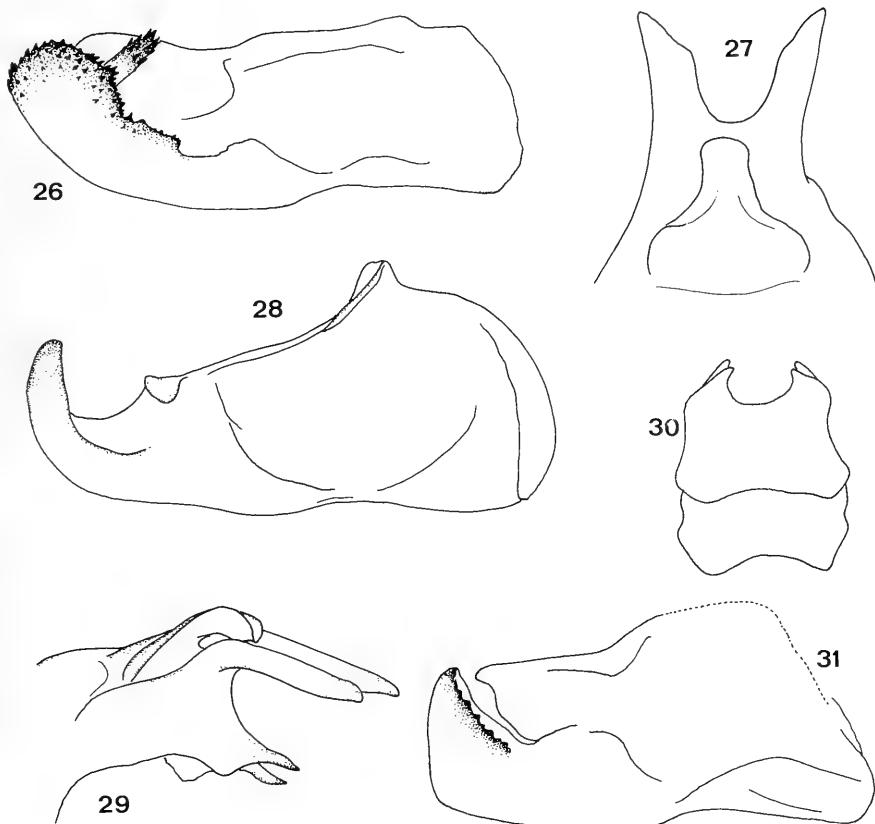


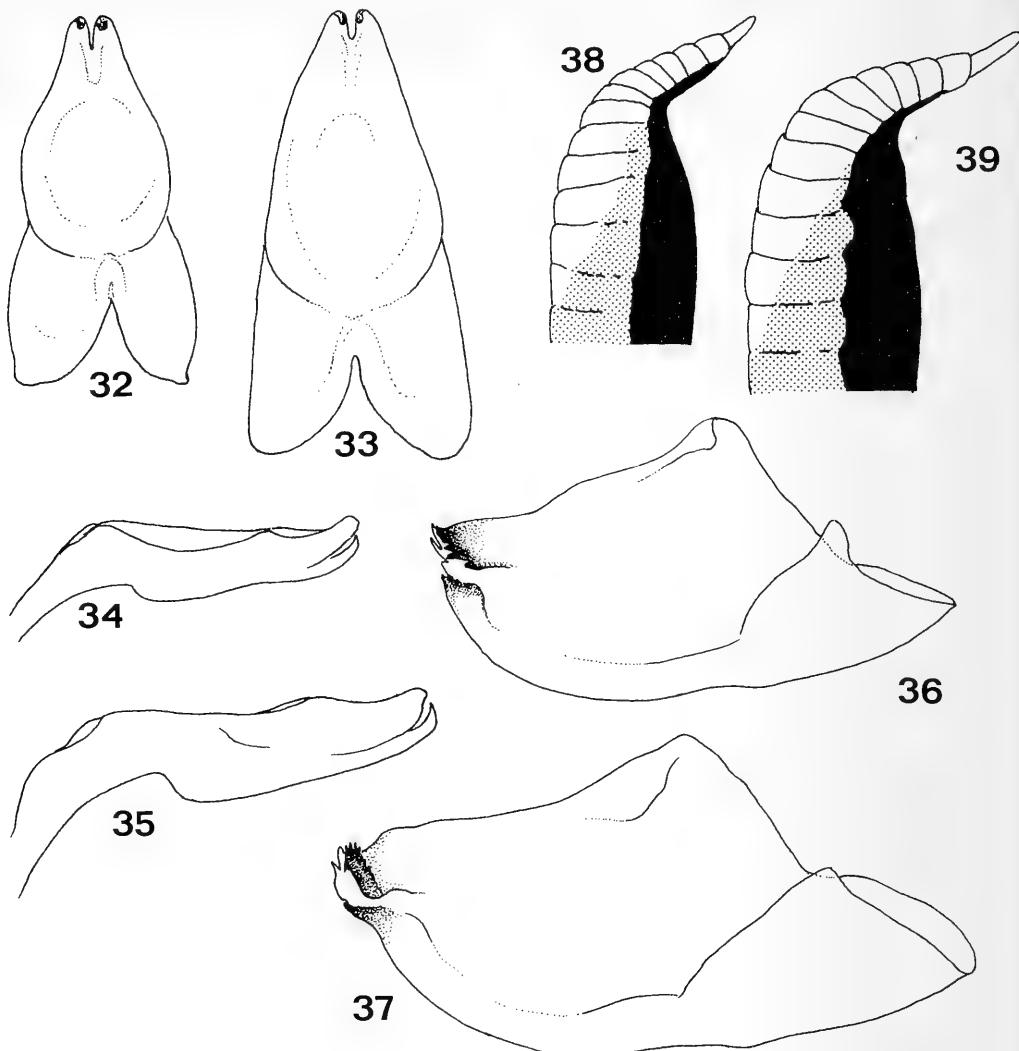
Fig. 26. *Eutychide subpunctata intermedia* subspec. nov., Paramaribo (Surinam), inside of left valva. Figs. 27—29, *Phlebodes meesi* spec. nov., Lely Gebergte (Surinam); 27, dorsal view of tegumen and uncus; 28, inside of left valva; 29, lateral view of tegumen, uncus and gnathos. Figs. 30—31, *Penicula criska extensa* subspec. nov., Linker Coppenname (Surinam); 30, dorsal view of tegumen and uncus; 31, inside of left valva. All figures drawn at same magnification.

only known from Peru, but in that species the cucullus is not as strongly bifurcate and the external characters are different, the colour being darker and the cell spot of the forewing being conjoined to the inner edge of the spot in space 2 (I do not understand why Evans, 1952, described *lactos* as a subspecies of *B. borax* Evans, as the genitalia are as different from those of *B. borax* as from those of any other *Bungalotis* species; it seems better to consider *lactos* a separate species).

Material examined. — Holotype, ♂, S. Surinam, Sipaliwini, air strip, 14.x.1968, at light, leg. E. H. Jonkers (RMNH).

15. *Bungalotis quadratum* Sepp, 1848.  
According to Evans (1952: 140) two subspe-

cies can be recognized, viz., ssp. *quadratum* (Honduras, Colombia, Guiana, Surinam), and spp. *barba* Evans (Fr. Guiana, Pará, Santarem, Peru). The differences in the male sex are as follows. In ssp. *quadratum* the ground colour is yellow and the costa of the hindwing ("upf" in Evans must be a misprint for "uph") broadly dark brown on the upper side. Ssp. *barba* is dark tawny, with dark brown area on upper side of hindwing usually limited to a small area under outer half of vein 7. One male from Paramaribo (RMNH) caught 5.i.1962, has the yellow colour of ssp. *quadratum* and the extension of the dark area on the upper side of the hindwing along the costa as in ssp. *barba*. The other male from Paramaribo (NZC) caught 23.x.1981, has the colour of ssp. *barba* and the extension of the



Figs. 32—39. *Polites vibicoides* spec. nov., Zanderij (Surinam) (even numbers), and *Polites vibex catilina*, Domburg (Surinam) (odd numbers); 32—33, dorsal view of tegumen and uncus; 34—35, lateral view of tegumen, uncus and gnathos; 36—37, inside of left valva; 38—39, apex of antennal club, black = with black scales, stippled = with orange-yellow scales, rest is nudum. All figures drawn at same magnification.

dark area of ssp. *quadratum*. This makes one wonder how far the subspecific distinction is justified.

#### 16. *Cogia hassan* Butler, 1870.

The specimens from Zanderij are all similar. They agree with ssp. *hassan* as defined by Evans (1953: 20), and also with the original description and figure of *Cogia freudiae* Williams & Bell, 1931, which Evans, in my opinion, justly

synonymized with *Cogia hassan* Butler. The shape of the valve, with the apex of the cucullus ending in a long spike, is exactly like the drawing by Williams & Bell (1931, fig. 3) and unlike the very schematic drawing by Evans (1953).

The single male from Temomairem, however, is different. The termen of the forewing is more convex and the lines on the underside of the hindwing are as described for ssp. *evansi* Bell, 1937, which according to Evans (1953) was fig-

ured by Draudt (1922, pl. 170d) under the name of "hassan" (the colours of Draudt's figure must have been invented by the printer, but the position of the lines on the underside of the hindwing is clear). The genitalia are similar to those of the specimens from Zanderij.

As Zanderij is in the north of the country and Temomairem in the extreme south, a subspecific difference does not seem to be too surprising. Ssp. *hassan*, however, is the subspecies of northern Brazil and ssp. *evansi* occurs in Bolivia and southern Brazil. The capture of a specimen with characters of ssp. *evansi* far within the boundaries of the distribution area of ssp. *hassan* suggests that the two taxa may be specifically distinct. On the other hand, they could also be merely seasonal forms. The material is still too scanty to make a firm statement.

#### 17. *Clito jonkersi* spec. nov.

External characters (fig. 55). — Male. Length of forewing 15.1 mm. Costal fold present. Nudum 22 segments. Forewing upper side dark brown with hyaline spots in spaces 1b (acco-lade-shaped), 2 (large, V-shaped), 3, 4, 5, and 6—8 (in line, the latter longer, extending further to termen), and in cell (U-shaped with rounded base). Hindwing upper side dark brown with hyaline spots in spaces 1c (anvil-shaped, just extending into space 1b), 2 (very small, at base), 6 (small, at base), 7 and in cell (filling more than half of cell); inner edge of spots in 1c, 7 and cell in line; faint whitish pointed submarginal spots in spaces 1c—6. Underside as upper side; lighter shading on forewing in spaces 1b—3 directly distad of the hyaline spots; also faint lighter shading along termen of hindwing in spaces 4—5.

Male genitalia (figs. 12, 13). — Gnathos relatively long, almost reaching apex of uncus. Cucullus stout, slightly higher than long, the broad apex strongly spined. Costal process short, stout, finely spined.

Identification. — Externally the new species comes closest to *C. littera anda* Evans, 1953. It differs in the white band of the hindwing being narrower and divided by dark veins, and the cell spot of the forewing not being rounded basally, but cut off obliquely. In *C. littera littera* Mabille, 1877, the white band of the hindwing is faint and the inner edge of the cell spot of the forewing forms a straight line perpendicular to the costa. The shape of the valve and length of the gnathos are different from those of all described *Clito* species.

Material examined. — Holotype, ♂, Domburg, 8.iii.1975, leg. E. H. Jonkers (RMNH).

Discussion. — According to Evans (1953) the genus *Clito* is characterized among other characters by a nudum of 16 segments. I don't know how Evans arrived at this figure. In the BM I checked the material arranged by Evans, and found the following numbers of nudum segments:

*C. littera* Mabille, ♂, 22; *C. bibulus* Riley, ♂ 18, ♀ 22; *C. clito* Fabricius, ♂ 18, ♀ 22; *C. sompa* Evans, ♂ 21; *C. zelotes* Hewitson, ♂ 21; *C. zenda* Evans, ♂ and ♀ 22; *C. tuva* Evans, ♂ and ♀ 22.

Apparently all species are rarely caught, judged from the very scanty material available.

#### 18. *Anthoptus epictetus* Fabricius, 1793.

According to Evans (1955: 62) the female should be entirely brown. However, in a series of 448 specimens he had only two females. In the series of 15 specimens from Surinam in RMNH there is a single female that is similar to the males except for a yellow stripe on the upper side of the hindwing from base to termen covering vein 1b.

#### 19. *Vinius tryhana* Kaye, 1913.

The three males in RMNH have identical genitalia corresponding with those of *V. tryhana*. One male has the tawny colour on the upper side more extensive, so that the cell of the hindwing is tawny, and the cell of the forewing is tawny with a narrow black central streak. By the latter character the specimen is similar to *V. exilis* Plötz, 1883, but the genitalia point definitely to *V. tryhana*.

#### 20. *Apaustus menes* Stoll, 1782.

According to Evans' (1955: 83) key, *Apaustus* has six nudum segments. In the description of the two species at p. 91, however, *A. gracilis* Felder is stated to have 4—6 and *A. menes* 8 nudum segments. The three specimens in RMNH which undoubtedly belong to *A. menes*, have 6 nudum segments.

#### 21. *Cymaenes geijskesi* spec. nov.

External characters (fig. 56). — Male. Length of forewing 12.4 mm. Upper side brown; forewing with faint ochreous spots in spaces 2, 3 and 6, and traces of spots in spaces 1b and 7, and in cell; hindwing practically unicoloured. Underside as upper side, a little paler, traces of

median spots in spaces 2—5 on the hindwing. Fringes sullied. Nudum with 13 segments of which 9 on apiculus.

Male genitalia (figs. 14—17). — Indentation of uncus not more than one third of total length of uncus + tegumen, twice as long as wide. Cucullus greatly expanded to a semicircle with a slightly serrate edge, turned over in horizontal position.

Identification. — Rather similar to *C. tripunctus* Herrich-Schäffer by the absence of markings in spaces 4 and 5 on the underside of the forewing, by the very faint cell spot on the forewing, the faint spots on the underside, and the broadened cucullus. It differs in being smaller (*C. tripunctus*, 13—15.3 mm), underside more yellowish than greyish brown, and abundantly in the genitalia, where the semicircular cucullus is unique for the genus and the indentation of the uncus is much narrower and shallower than in *C. tripunctus*, in which moreover the uncus bulges strongly laterally. In *C. tripunctus*, and according to Evans (1955) in all other *Cymaenes* species as well, the nudum consists of 11 segments, of which 8 are on the apiculus. In *C. geijskesi* there are two more segments. As the number of nudum segments may vary even within a species, examination of much more material is needed to make sure that this is a constant difference between the new species and its congeners.

Material examined. — Holotype, ♂, Surinam, Paramaribo-Zanderij, savanne, 27—30.viii. 1964, leg. D. C. Geijskes (RMNH).

## 22. *Vehilius major* spec. nov.

External characters (figs. 57, 58). — Male. Length of forewing 13.4 mm. Exactly like *V. vetulus* Mabille, only larger (*V. vetulus* 10—12.2 mm) and upper cell spot on upper side of forewing more conspicuous.

Male genitalia (figs. 18, 19). — Similar to those of *V. vetulus*, but outline of valve trapezoid rather than triangular as in *V. vetulus*.

Material examined. — Holotype, ♂, Surinam, Patamakka Rivier, 4.ix.1969, leg. E. H. Jonkers (RMNH).

## 23. *Mnasilus allubita* Butler, 1877, and *Nastra guianae* Lindsey, 1925.

*M. allubita* is very difficult to separate from *N. guianae*. The only external difference I could find is the colour of the palps and cheeks, white in *N. guianae*, cream-coloured or pale yellow in

*M. allubita*. According to Evans (1955) the only difference between *Nastra* and *Mnasilus* is the occurrence of a recumbent hair tuft on the upper side of the forewing in males of *Mnasilus*. This is correct, but little obvious. It seems exaggerated to base a generic distinction on this character only. Together with related genera these two are badly in need of revision.

## 24. *Mnasitheus similis* spec. nov.

External characters (figs. 20, 59, 60). — Male. Length of forewing 12.5 mm. Upper side entirely dark brown, no spots; slight greenish metallic sheen on head, collar and thorax. Underside dark brown, faintly lighter in tornal half of forewing, in spaces 1a—c of hindwing, and with very faint discal spots in spaces 2—6 of hindwing. Forewing with tripartite stigma: a short, obliquely set patch at the base of space 2 and directly under it, a small patch in upper half of space 1b and a patch in lower half of space 1b similar to that in space 2.

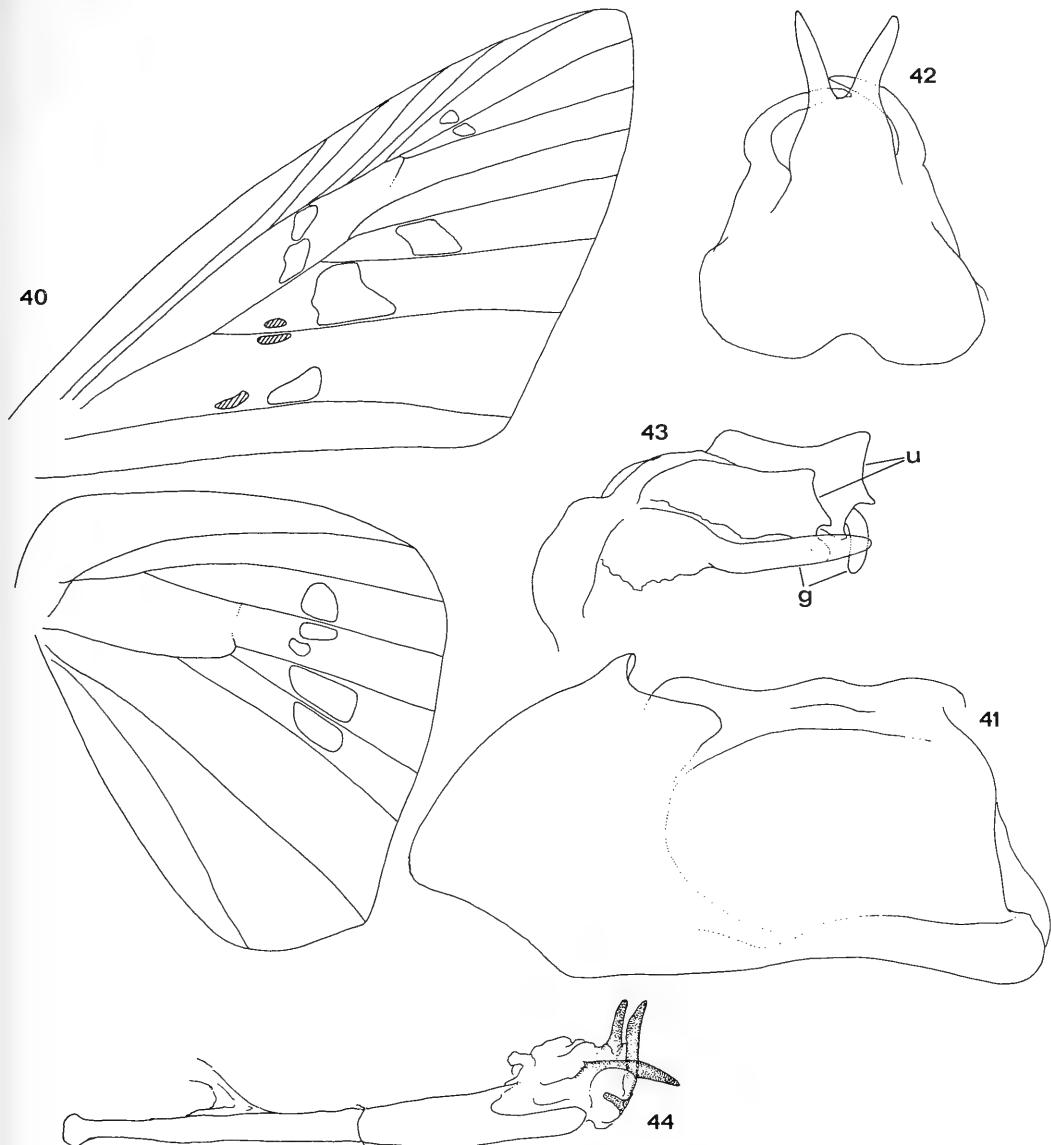
Male genitalia (figs. 21, 22). — Uncus deeply indented. Valve with cucullus strongly developed in dorso-proximal part, extending far beyond the ill-developed costa; apex of cucullus upturned and pointed.

Identification. — With Evans (1955) the new species keys more or less to *M. simplicissima* Herrich-Schäffer, which however has an entire uncus and a differently shaped cucullus, without the strong dorso-proximal expansion. The shape of the cucullus is reminiscent of that of *M. forma* Evans, which does not have the deeply indented uncus of the present species. The shape of the tripartite stigma differs from that of any other *Mnasitheus* species, the patches in space 1b usually being parallel to vein 1, or (in *M. continua* Evans) perpendicular to vein 1, and the patch in space 2 either parallel to vein 2 or to the cubitus.

Material examined. — Holotype, ♂, Surinam, leg. E. H. Jonkers (RMNH).

## 25. *Papias phainis* Godman, 1900.

The single female was identified as belonging to this species rather than to *P. phaeomelas* Geyer because of the palps being yellower and the hindwing having well visible spots on the underside. Generally, identification of females of this genus as well as of many related genera is hampered by the fact that the female genitalia have not been studied comparatively (and usually are not known at all).

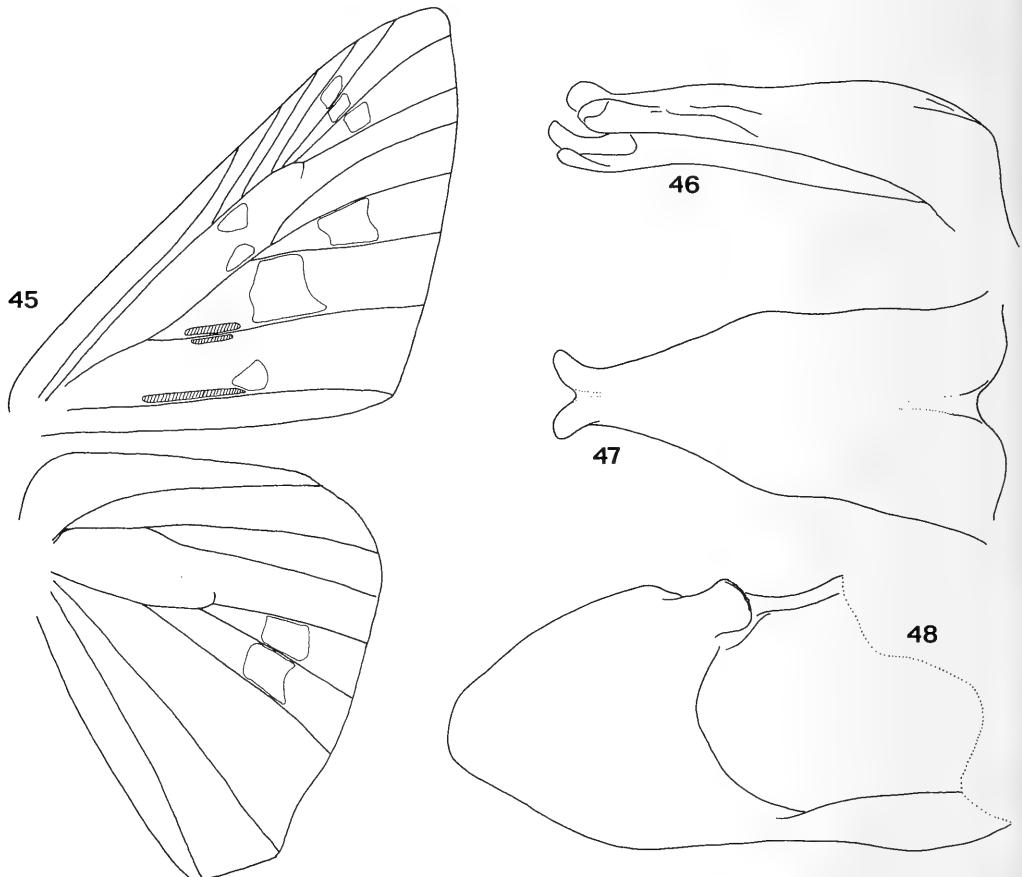


Figs. 40—44. *Cravera rara* gen. et spec. nov., Zanderij (Surinam); 40, wing venation of male, spots and brands (hatched) of upperside indicated; 41, inside of left valva; 42, dorsal view of tegumen and uncus; 43, lateral view of tegumen, uncus (u) and gnathos (g); 44, aedeagus. Figs. 41—43 drawn at twice the magnification of fig. 44.

#### 26. *Cobalopsis dorpa* spec. nov.

External characters (figs. 61, 62). — Male. Length of forewing 16.2 mm. Upper side forewing dark brown; basal third with inconspicuous dark yellow hairs and scaling; semi-hyaline spots in spaces 2, 3 and 6—8, the latter in line (the spot in space 8 is inconspicuous); an

opaque spot over vein 1 just beyond middle; fringes pale brown, dark brown at the end of veins. Upper side hindwing dark brown; inconspicuous dark yellow hairs and scaling in cell and spaces 1c—5; fringes as on forewing. Underside forewing as upper side, narrowly violet along apical half of termen and in spaces 4—5



Figs. 45—48. *Surina unica* gen. et spec. nov., Surinam; 45, wing venation of male, spots and brands (hatched) of upperside indicated; 46, lateral view of tegumen, uncus and gnathos; 47, dorsal view of tegumen and uncus; 48, inside of left valva. Parts of genitalia drawn at same magnification.

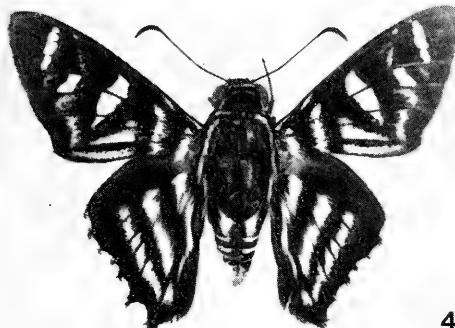
midway between the apical spots and termen; area between apical spots and violet scaling along termen darker than rest of wing; fine dark brown terminal line. Underside of hindwing dark brown, veins pale brown; violet scaling along termen, separated from fringes by fine dark brown terminal line; pale median spots with a violet-greyish tinge and whitish outlined in spaces 1b—7, and similar spots in cell and at base of space 7 (vaguely continued into cell and space 8); spot in space 6 detached from both the spot in space 5 and the cell spot; median spot in space 7 large, completely overlapping the spot in space 6; cell spot midway between the basal and median spots in space 7 and detached from either.

Female. As male, but spots slightly larger,

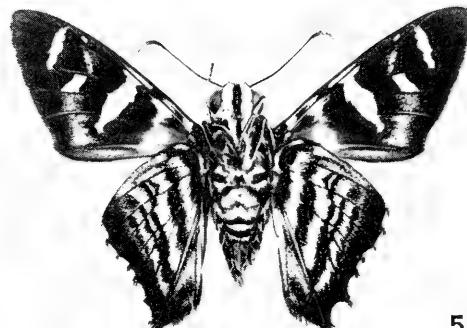
and on upper side of forewing with faint yellowish spots in spaces 4—5, almost midway the apical spots and termen.

Male genitalia (fig. 23). — Uncus and gnathos bipartite as in other species of the genus. Aedeagus dorso-apically with two longitudinal rows of strong spines. Valve peculiarly shaped, more or less like a shoe in lateral view; cucullus occupies more than half of entire valve, dorsal and ventral edge parallel, slightly serrate along ventral edge, apex obtuse. Costa weakly developed; no costal process.

Identification. — The new species agrees with the description of *C. prado* Evans, but comparison with the type and further material of the latter species in the BM revealed that in *C. prado* the underside of the hindwing is dark brown



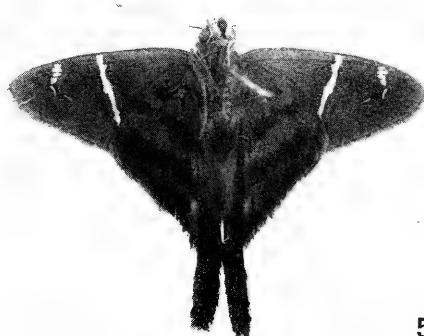
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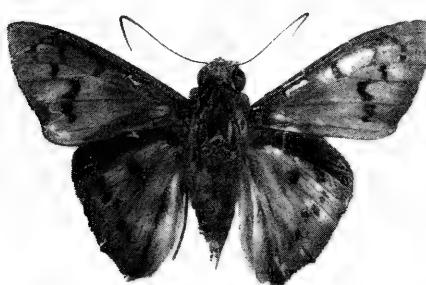
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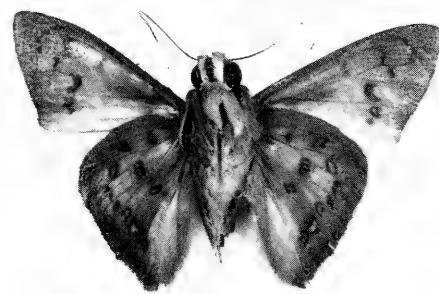
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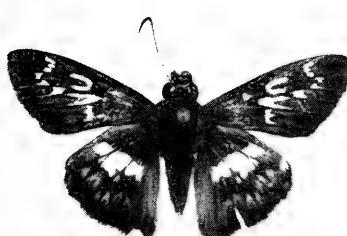
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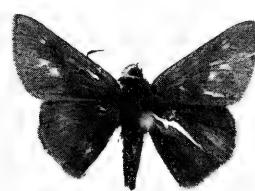
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Figs. 49, 50. *Elbella bicuspis* spec. nov., holotype, upper- and underside. Figs. 51, 52. *Urbanus ambiguus* spec. nov., holotype, upper- and underside. Figs. 53, 54. *Bungalotis sipa* spec. nov., holotype, upper- and underside. Fig. 55. *Clito jonkersi* spec. nov., holotype, upperside. Fig. 56. *Cymaenes geijskesi* spec. nov., holotype, upperside.



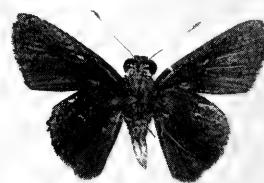
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Figs. 57, 58. *Vehilius major* spec. nov., holotype, upper- and underside. Figs. 59, 60. *Mnasitheus similis*, spec. nov., holotype, upper- and underside. Figs. 61, 62. *Cabalopsis dorpa* spec. nov., holotype, upper- and underside. Fig. 63. *Cabalopsis tanna* spec. nov., holotype, upperside.

with faint lighter brown spots. The markings of the new species are more similar to those of *C. catocala* Herrich-Schäffer, which, however, has the spot in space 6 on the underside of the hindwing attached to the spot in space 5 and detached from the spot in space 7. In the much smaller *C. dagon* Evans, the spots are arranged as in *C. dorpa* except that in the former species the spots in spaces 6 and 7 are conjoined to the cell spot. The shape of the valve of *C. dorpa* is not found in any other *Cobalopsis* species.

Material examined. — Holotype, ♂, Surinam, Paramaribo, 3.viii.1963, leg. E. H. Jonkers. Paratype, ♀, Surinam, Paramaribo, Ma Retraite, 1.x.1960, leg. E. H. Jonkers. Both types in RMNH.

### 27. *Cobalopsis tanna* spec. nov.

External characters (fig. 63). — Male. Length of forewing 13.5 mm. Nudum occupying 12 segments of which 9 on apiculus. Mid tibiae sparsely spined. No secondary sex characters. Upper side of forewing brown, possibly with yellowish basal clothing but specimen too worn to make sure; hyaline white spots in spaces 2, 3, 6, and in lower half of cell over origin of vein 3; spot in space 2 slightly closer to cell spot than to spot in space 3; a yellowish opaque spot in space 1b, and a trace of a minute dot in space 7. Upper side hindwing brown with yellowish clothing over greater part of the wing; no spots. Underside of both wings brown, markings as on upper side.

Male genitalia (figs. 24, 25). — Uncus and gnathos bifid, uncus arms more widely apart than gnathos arms. Valve seemingly trapezoid in lateral view because apex turns inward.

Identification. — The new species agrees well with the description of *Cobalopsis* as given by Evans (1955), but it does not fit any of the described species of the genus. As the specimen was collected in a Malaise trap, its condition is rather poor, but it is good enough to make sure that there are no spots on the hindwing. The only known *Cobalopsis* species with an unmarked hindwing is *C. dedecora* Plötz, which has the underside of the hindwing reddish-grey and in the forewing only spots in spaces 3, 6 and 7. The presence of a lower spot only in the cell is unique in *Cobalopsis*. Upper cell spots are found in *C. autumna* Plötz and *C. nero* Herrich-Schäffer, while the female of the first-mentioned species has a lower cell spot as well; these two species have spots on the underside of

the hindwing, and their genitalia are quite different, the cucullus being long and narrow.

Material examined. — Holotype, ♂, Surinam, Domburg, 18—23.xii.1963, Malaise trap, leg. D. C. Geijskes (RMNH).

### 28. *Morys subgrisea paradoxa* subspec. nov.

External characters. — Male. Length of forewing 12.5 mm. Upper and underside uniform dark brown. On upper and underside of forewing very faint spots in spaces 2 and 3, and almost invisible in space 6. Faintest traces of median spots on the underside of the hindwing. Stigma on forewing and genitalia as in *M. subgrisea subgrisea* Mabille. In size it is closer to the only other described subspecies, *M. subgrisea prada* Evans (cf. Evans, 1955: 168). It can be distinguished by the almost complete lack of spots and by the lack of grey scaling on the underside of the hindwing, so that the name *subgrisea* is not very appropriate, hence the proposed subspecies name.

Material examined. — Holotype, ♂, Surinam, Zanderij, savanne, 13—16.viii.1964, leg. D. C. Geijskes (RMNH).

### 29. *Vettius yalta* Evans, 1955.

The two females directly key to *V. artona* Hewitson or *V. yalta* Evans with Evans (1955). They differ from the female of *V. artona* in being smaller (length of forewing 14—16.4 mm, as against 17.8 mm), in having the spot in space 2 of the forewing more or less under the cell spots (in *V. artona* mid cell spots and spot in space 3), and in having a paler underside of the hindwing. There are also differences in the genitalia. The allocation of the two specimens to *V. yalta* must be considered preliminary.

### 30. *Eutychide subpunctata intermedia* subspec. nov.

Discussion. — The three specimens agree with the original description of *E. sempa* Evans, 1955, except for the cucullus being serrate (fig. 26). Examination of the type and the only other available male of *sempa* in the BM, however, revealed that also in *E. sempa* the cucullus is serrate, be it less obvious than in *E. subpunctata* Hayward. The spined dorsal projection of the cucullus, according to Evans' figures present in *E. sempa* and absent in *E. subpunctata*, was possibly broken in the left valve figured by Evans, as it is present in the right valve of the only specimen of *E. subpunctata* studied by Evans,

more or less concealed by the strong serration of the cucullus. Further differences between *E. sempa* and *E. subpunctata* are found in the uncus arms, which are about parallel in *E. sempa* and divergent in *E. subpunctata*, and in the colour of the wings, *E. sempa* being darker but with paler area along dorsum on the underside of the forewing, and of the cilia which are paler in *E. subpunctata*.

So far, *E. subpunctata* and *E. sempa* are well-defined separate entities. However, the three specimens from Surinam are not only topographically intermediate (*E. sempa* is only known from Guiana, *E. subpunctata* from Argentine and French Guiana), but also morphologically. The cucullus is more rounded than in both *E. sempa* and *E. subpunctata*, the serration is intermediate. The uncus arms are more or less parallel. The pale dorsal area on the underside of the forewing is inconspicuous. The cilia are brownish grey.

On the basis of the taxonomically as well as geographically intermediate position of the Surinam specimens, it seems most appropriate to unite *E. sempa* and *E. subpunctata* with the Surinam representatives into a single, geographically variable species. The Surinam specimens are sufficiently different (see above) to warrant subspecific distinction; the subspecies is named *Eutychide subpunctata intermedia* here.

Thus *E. subpunctata* consists of the following subspecies: *E. subpunctata subpunctata* Hayward (Argentine, French Guiana), *E. subpunctata intermedia* subspc. nov. (Surinam), and *E. subpunctata sempa* Evans (comb. nov.) (Guiana).

Material examined. — *E. subpunctata subpunctata*: 1 ♂, French Guiana (BM). *E. subpunctata intermedia*: holotype, ♂, Surinam, Paramaribo, Ma Retraite, 6—8.i.1964, leg. D. C. Geijskes; 2 ♂, paratypes, same data but 14—16.i.1964 and 4—8.iii.1964, respectively (all types in RMNH). *E. subpunctata sempa*: 2 ♂, 1 ♀, Guiana, Takutu River (incl. holotype, ♂) (BM).

### 31. *Talides sinois* Hübner, 1819.

The differences between this species and *T. alternata* Bell are slight. Moreover, the differentiating characters given by Evans (1955: 226—227) are liable to variation. In the four males from Surinam in the RMNH belonging to *T. sinois* and/or *T. alternata*, the shape of the cucullus as well as the length of the tegumen spike is different for each male. There is also

variation in the distance between spots 2 and 3 of the forewing. It makes one wonder if *T. sinois* and *T. alternata* are really separate species. The material listed has been assigned to the two species according to the closest match with Evans' descriptions, but especially for the males assigned to *T. sinois*, this match is not perfect. The single female has been listed provisionally under *T. sinois*, no differentiating characters having been published for the female sex.

### 32. *Carystus elvira* Plötz, 1882.

Evans (1955) who had no material of this species at his disposal remarked: "May be an aberration or a faulty figure", a rather bold statement for an author who had not seen any specimens. It is true that the figure in Draudt (1923, pl. 189b) does not seem to have entirely right colours, but Evans could not know this. Moreover, the colour differences between Draudt's figure (probably based on the original figure by Plötz) and the specimen in the RMNH may be a sexual difference, the figure representing a male and the RMNH specimen being female.

The female in the RMNH can be described as follows. Head with a conspicuous white spot directly behind the antennae. Length of forewing, 21.4 mm. Basal third of costa of forewing, patagia and tegulae with orange hairs. Upper side of forewing brown with sharply defined hyaline spots in spaces 1b (against vein 1), 2, 3, 6 and 7 (last two small, especially in space 7), and two spots in cell slightly basad of spot in space 2. Upper side hindwing brown, light band from base to termen on underside weakly shining through. Underside of forewing as upper side, but orange along costa up to end of vein 12, from there a dull yellowish subapical band, overlapping the spots in spaces 6 and 7 (making them obscure) and ending at termen in space 4/5; pale yellowish suffusion from the spot in space 1b towards the termen. Underside of hindwing with a warm brown-yellow colour, paler dull yellow from base through cell and space 4/5 to termen, this pale band flanked by dark brown colouring which extends more or less along the veins; space 1b greyish brown.

### 33. *Carystoides basoches* Latreille, 1824.

The males agree with *C. basoches*. The females in RMNH differ in size (forewing, 20.1 and 21.5 mm) and spotting: in the smaller specimen the hyaline central spot on the upper side of the hindwing is relatively small and contin-

ued across space 3, in the larger specimen it is a little larger and confined to spaces 4—5. Thus, both females have some characters of *C. basoches* and some of *C. noseda* Hewitson. As the males are undoubtedly *C. basoches*, I have placed the females here as well.

34. *Perichares deceptus* Butler & Druce, 1872.

The cell spots of the forewing are separate in the single male from Surinam. This is a common feature in ssp. *drina* Evans, but also occurs in ssp. *luscinia* Plötz. The lilacine areas on the underside of the hindwing concord with the situation in ssp. *luscinia* (which is only known from S. Brazil). In view of its locality, one would expect the Surinam specimen to be closest to ssp. *fulvimargo* Butler, which occurs in Colombia, Venezuela, Ecuador and Peru, but the yellow colour at the tornus of the hindwing, characteristic of ssp. *fulvimargo*, does not occur in the Surinam specimen. More and better preserved material is needed to decide on the systematic position of the population in Surinam.

35. *Phlebodes meesi* spec. nov.

Only a male available. External characters. — Length of forewing, 15.3 mm. Upper side very dark brown; inconspicuous dark ochreous hairs at base of forewing; hyaline spots only in spaces 2 and 3, spot in space 2 larger and less regular than square spot in space 3; no other spots excepting a very faint spot in space 1b indicated by some pale ochreous scales close to vein 1 just beyond its middle; hindwing unmarked. Underside forewing as upper side, purplish in apical area. Underside hindwing dark brown with purplish gloss, but space 1b and greater part of space 1c plain brown; veins a little paler, no spots. Forewing with sagittate brand over origin of vein 2, and a long narrow brand under basal third of vein 2.

Genitalia (figs. 27—29). — Uncus bifid, arms about three times as long as wide, slightly diverging. Tegumen with central process, broad at base, much narrower in distal half, bluntly ended, not reaching base of indentation of uncus. Gnathos consisting of two separate, sharply pointed sclerites. Cucullus with long, narrow, upturned apex; costa hardly developed, at distal end with short, inwards curving flap over basal part of cucullus.

Material examined. — Holotype, ♂, Surinam, Lely Geberge, 600—700 m, 30.x.1979, leg. G. F. Mees. In RMNH.

**Discussion.** — *P. meesi* differs from all other *Phlebodes* species (excepting some specimens of the South Brazilian *P. smithi*) in the absence of apical spots of the forewing and of any spots on upper and underside of the hindwing. In the genitalia the new species seems to come close to *P. vira* Butler, 1870, *P. virgo* Evans, 1955, and *P. torax* Evans, 1955, although in the genitalic drawings by Evans (1955) no trace can be seen of the central process of the tegumen. External- ly these species differ from *P. meesi* in the underside of the hindwing being ochreous-brown with conspicuous yellow veins.

36. *Cyneia cyrus* Plötz, 1883.

The two specimens are more like ssp. *hippo* Evans, described from Trinidad, than ssp. *rhino* Evans, described from French Guiana, Upper Amazons and Pará. Length of forewing 21.2 mm. No spot in space 1b on the upper side of the forewing; apical spots in spaces 6—8 (almost invisible in one specimen). Underside hindwing, spots in spaces 2 and 3 very faint.

37. *Penicula criska extensa* subspec. nov.

Description (figs. 30, 31). — Male. Externally and in the genitalia similar to *P. criska* Evans, but differs in the shape of the valva, where the cucullus is expanded disto-ventrally, so that the distal edge is almost perpendicular to the ventral edge, and apex not extending above costa. In *P. criska criska* the ventral edge of the cucullus gently curves to the apex which extends above the costa.

Material examined. — Holotype, ♂, Linker Coppenname, Zuidkreek 11.viii.1943, at light, leg. D. C. Geijskes. In RMNH.

38. *Polites vibex* Geyer, 1832.

The extension of the tawny spots is variable, so that it is not well possible to make a sharp distinction between ssp. *praeceps* Scudder and ssp. *catilina* Plötz. This may be due to the fact that Surinam is in the area where both subspecies meet, from Ecuador through Venezuela to the Guianas.

39. *Polites vibicoides* spec. nov.

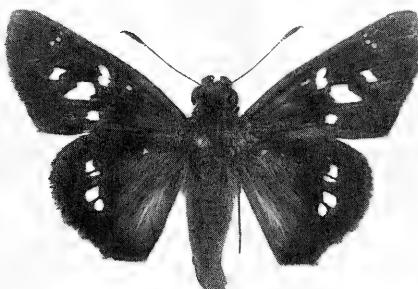
External characters (figs. 64, 65). — A small replica of *P. vibex praeceps/catilina*. Male. Length of forewing, 10.3—10.5 mm. Markings exactly as in *P. vibex*, but tawny colour slightly darker and warmer. Extension of tawny colour on upper side variable; median band of forewing may be narrower than dark terminal area.



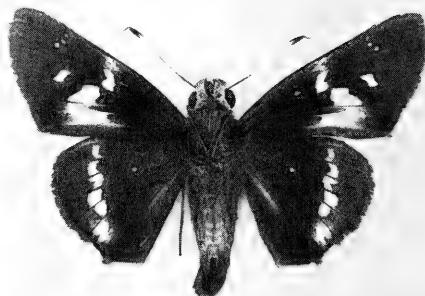
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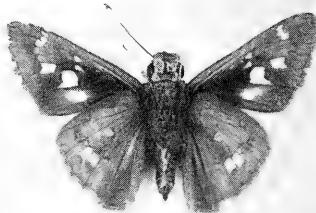
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69

Figs. 64, 65. *Polites vibicoides* spec. nov., holotype, upper- and underside. Figs. 66, 67. *Cravera rara* gen. et spec. nov., paratype, upper- and underside. Figs. 68, 69. *Surina unica* gen. et spec. nov., holotype, upper- and underside.

Female as large as male; on underside of hindwing band of yellow median spots from vein 2 to vein 8, flanked by dark brown spots in spaces 2, 3, 6 and 7, quite different from the dull greyish-ochreous colours of *P. vibex catilina* females.

Male genitalia (figs. 32—37). — Similar to *P. vibex*. Uncus and tegumen more rounded in dorsal view. Cucullus and costa of valve not

suddenly narrowing as in *P. vibex*. Costa broadened and hollowed apically so as to receive the apex of the cucullus; apical spines of costa directed caudad or more or less turned up as in *P. vibex*. The complex aedeagus is also similar to the structure found in *P. vibex*.

Identification. — *Polites* is a mainly North American genus consisting of seven species (Evans, 1955). The only species up to now

known to occur in South America is *P. vibex* (distributed from the northeastern U.S.A. to Argentina). The new species cannot be mistaken for *P. vibex* because it is much smaller (*P. vibex* from Surinam, length of forewing 13.8–14.8 mm). For the rest, however, they are so similar that they could be considered subspecies if they were not sympatric.

Material examined. — Holotype, ♂, Surinam, Zanderij, savanne, 27–30.viii.1964, leg. D. C. Geijskes. Paratypes, 4 ♂, 2 ♀, same data but 16–20.viii.1964 (1 ♂), 20–24.viii.1964 (1 ♂, 1 ♀), 24–26.viii.1964 (1 ♂, 1 ♀), 4–7.ix.1964 (1 ♂). All types in RMNH.

Remark. — According to Evans (1955) the *Polites* species have 11–12 nudum segments. This may hold true for North American species, but in the Surinam specimens of *P. vibex* and *P. vibicoides* the number of nudum segments is 13 (figs. 38, 39).

#### 40. *Panoquina panoquinoides minima* sub-spec. nov.

External characters. — Length of forewing 10.5–11.7 mm. Upper side forewing brown, overlaid with yellow scales and hairs along costa and in basal third. Pale yellow opaque spot in space 1b, pale yellow hyaline spots in spaces 2 and 3, inconspicuous apical spots in spaces 6 and 7 (one or both may be absent); fringes pale ochreous. Upper side hindwing brown overlaid with yellow hairs and scales; fringes pale ochreous. Underside forewing as upper side, darker brown in basal third. Underside hindwing greyish brown, veins pale yellow, no spots or at most traces of inconspicuous, streaklike, pale yellow spots in spaces 2 and 3.

Male genitalia. — As in *P. panoquinoides* Skinner.

Identification. — Because of its small size it was surprising to find that the new subspecies belonged to a *Panoquina* species. With 12–14.3 mm for the already described subspecies, *P. panoquinoides* is the smallest member of the genus, the other species varying from 16 to 25 mm. Apart from its size the new subspecies is characterized by the reduction (in most specimens complete absence) of spots on the hindwing.

Material examined. — Holotype, ♂, Parwabos, Kwattaweg naar zee, 8–11.ii.1964, in Malaise trap, leg. D. C. Geijskes. Paratypes: 1 ♂, Paramaribo; 11 ♂, 2 ♀, same data as holotype, but 1–4.ii.1964 (1 ♂), 8–11.ii.1964 (2 ♂), 11–14.ii.1964 (3 ♂), 14–18.ii.1964 (1 ♂), 18–

24.ii.1964 (1 ♂), 29.ii–2.iii.1964 (1 ♂, 1 ♀), 3–6.iii.1964 (2 ♂, 1 ♀); 3 ♂, Matapica in Malaise trap. All types in RMNH.

#### 41. *Cravera* gen. nov.

External characters. — Palpi second segment flattened, third short, hardly protruding above clothing of second segment. Antennae reaching to origin of vein 10. Antennal club swollen, three times as wide as antennal shaft, length 5/18 of total length of antenna, constricted before apiculus which is almost twice as long as width of club. Nudum covering 15 segments of which 9 on apiculus. Forewing cell almost as long as dorsum; vein 2 closer to vein 3 than to base; vein 4 midway between veins 3 and 5; vein 5 decurved at origin towards vein 4; termen almost straight from vein 6 to vein 1, very slightly incurved in space 1b; white hyaline spots in spaces 1b, 2, 3, 6–7, 8 (may be absent) and cell; spots in 6 and 7 directed to upper half of termen. Hindwing cell about half as long as wing measured along vein 4; vein 7 originates much closer to base than vein 2; termen almost straight (in female slightly curved) from vein 7 to vein 1b; vein 1b produced, longer than vein 1a; white hyaline spots in spaces 2, 3, 5 and 6. Hind tibiae with upper pair of spurs absent. Abdomen as long as vein 1a of hindwing. Male with short inconspicuous stigmas over and under basal 1/4 of vein 2 and over basal half of vein 1 of forewing (fig. 40). Female with dense long hairs at tip of abdomen.

Male genitalia. — Uncus and gnathos bipartite; apex of aedeagus with complicate processes and horns.

Discussion. — See after description of the type-species.

Type-species. — *Cravera rara* spec. nov.

#### *Cravera rara* spec. nov.

External characters (figs. 66, 67). — Male. Length of forewing 23.9 mm. Upper side black. Forewing cell spot consisting of two spots which just touch and are placed almost parallel to termen. Hindwing with very small spot in space 4. Thorax, abdomen, base of forewing to origin of vein 2, and basal half of hindwing with bluish-grey hairs. Underside brown. Forewing on underside with white suffusion along costa over cell spot, and extensive white suffusion in space 1b under the spot in space 2 distally from and in continuation with the spot in space 1b. Hindwing on underside in addition to the hyaline spots white patches in space 1c (large, be-

tween spot in space 2 and termen) and space 7 (small, in line with other spots), and a white dot just before end cell. Fringes dark brown, white on forewing at space 1b and on hindwing at spaces 1b, 1c and, very narrowly, 2. Palpi and underside abdomen greyish, underside thorax pale bluish-grey. Antennae upper side at base of club and basal half of shaft chequered, rest black; underside white on basal half of club and upper half of shaft, rest black.

Female. Length of forewing 25.5 mm. As male. Cell spot forewing undivided. Hindwing underside with same spots as male, but upper side no spot in space 4.

Male genitalia (figs. 41—44). — Tegumen short and broad, with a central indentation in proximal edge, so that proximal part appears to be bilobed. Uncus dorsally with a gutterlike longitudinal depression ending in an apical indentation, the two apical processes very much flattened laterally and expanded dorso-ventrally. Gnathos consisting of two long, strongly incurving arms, as long as uncus. Valve trapezoidal, cucullus squarish; dorso-distal corner of cucullus slightly prolonged and twisted; dorso-proximal corner overlapped by the weakly developed costa. Aedeagus apically with long curved horns.

Identification. — Externally the present species seems close to *Xeniades laureatus* Draudt, 1924, known only from a single male caught at Songo (Bolivia). If ever the type of the latter species will turn up, it might prove to belong to the same genus. Differences are found in the presence of a suffused white band externally of the hyaline spots on the underside of the hindwing, white underside of body and palpi and dark green upperside of body and wing bases in *X. laureatus*. The differences could even be subspecific, but without having studied the type, one cannot be sure.

Material examined. — Holotype, ♂, Surinam, Zanderij, Savannenbos, 28.i.1962, leg. E. H. Jonkers. Paratype, ♀, same data. Both types in RMNH.

Discussion. — The new genus is undoubtedly closely related to *Xeniades*, in which genus the apex of the aedeagus can also be provided with long processes. It differs, however, in the absence of the upper pair of spurs on the hind tibiae, the shorter hindwing cell, the black instead of brown colour of the upper side, the white instead of yellow spots on the upper side of the hindwing, and the direction of the white band on the underside of the hindwing towards the

outer instead of the basal part of vein 8.

Evans (1955) without having seen the type of *X. laureatus* nor any additional material, transferred this species to the genus *Vacerra*, which differs from *Cravera* in the possession of the upper pair of spurs on the hind tibiae, in the spots in spaces 6 and 7 of the forewing being directed to the lower half of the termen, and in the possession in the male of a long stigma over basal half of vein 1 of the forewing and at most an additional short stigma under basal quarter of vein 2.

#### 42. *Surina* gen. nov.

External characters. — Male. Palpi flattened. Antennae longer than half length of forewing, reaching to about origin of vein 9; antennal club constricted before the angled apiculus; nudum 14 segments of which 8 on apiculus. Forewing and hindwing with hyaline spots. Forewing with linear stigmas on both sides of vein 2 and over vein 1. Cell of forewing as long as dorsum. Cell of hindwing just over half wing; termen straight, slightly excavate in space 1c; vein 1a shorter than vein 1b. Abdomen shorter than dorsum of hindwing. Mid tibiae spined. Hind tibia with the usual two pairs of spurs.

Discussion. — See after description of type-species.

Type-species. — *Surina unica* spec. nov.

#### *Surina unica* spec. nov.

External characters (figs. 45, 68, 69). — Male. Length of forewing 18.9 mm. Forewing upper side brown; ochreous superscaling in basal part, especially along costa; pale yellowish hyaline spots in spaces 1b (against vein 1), 2, 3, 6—8 and two small spots in cell; spot in space 6 slightly out of line with spots in spaces 7 and 8, towards termen; fringes brown, paler towards tornus. Hindwing upper side brown, basal hairs more ochreous tinged; conspicuous, whitish, hyaline spots in spaces 2 and 3, and a vague spot at end cell; fringes pale brown. Forewing underside brown, paler brown along costa and termen down to vein 2, and from costa to spot 3, leaving a narrow darker brown area from outside spot in space 3 to spot in space 6; spotting as on upper side, but spot in space 1b in a suffused white patch. Underside hindwing pale brown; spots as on upper side, spot end cell more conspicuous; indications of small spots in spaces 4—7; ground colour slightly darker around spots. Forewing upper side with a long narrow stigma over vein 1 from just under the spot in

space 1b towards base, and narrow stigmas on both sides of vein 2 between the spot in space 2 and the origin of vein 2.

Male genitalia (figs. 46—48). — Uncus slightly indented; arms divergent, flattened laterally. Gnathos also bifid, just reaching beyond uncus. Cucullus expanded, dorso-proximally with a rounded projection over the weakly developed costa. Aedeagus ventrally broad and flattened; a big, spiky cornutus.

Material examined. — Holotype, ♂, Surinam, leg. Tengberg (RMNH).

Discussion. — The flattened palpi, constricted antennal club and straight termen of hindwing readily distinguish the species as a member of the *Calpodess* group (Evans, 1955: 398). It fits, however, none of the genera which are recognized in this group. In *Vacerra*, e.g., the cell of the forewing is shorter, the abdomen as long as the dorsum of the hindwing, the stigmas are different, and the apical spots of the forewing are exactly in line. In *Niconiades* the cell of the forewing is also shorter and the stigmas different, while generally vein 1a of the hindwing is longer than vein 1b. *Xeniades* has more nudum segments, and a conspicuous white band on the underside of the hindwing. *Neoxeniades* has also more nudum segments, and the wing bases blue or green. Also the genitalia do not give a clue as to which genus the new species could belong, so that I decided to erect a new genus for it. A revision of the whole *Caldodes* group would be needed to establish the relationships between the genera.

#### 43. *Neoxeniades cincia* Hewitson, 1871.

The male and female agree entirely with the description of this species in Evans (1955), but they have a single cell spot in the forewing. Examination of the three specimens in the BM (all from Pará) showed that also in this material there is a single cell spot, and it is not clear why Evans mentioned "a double hyaline white spot in cell".

#### 44. *Neoxeniades braesia* Hewitson, 1867.

According to Evans (1955) the cell spot of the forewing is divided in ssp. *braesia* to which subspecies the specimen from Surinam geographically should belong. This specimen, however, has the cell spot undivided. For the rest it agrees completely with the description.

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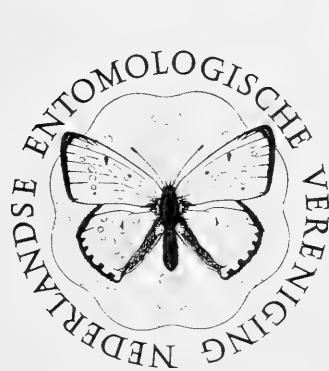
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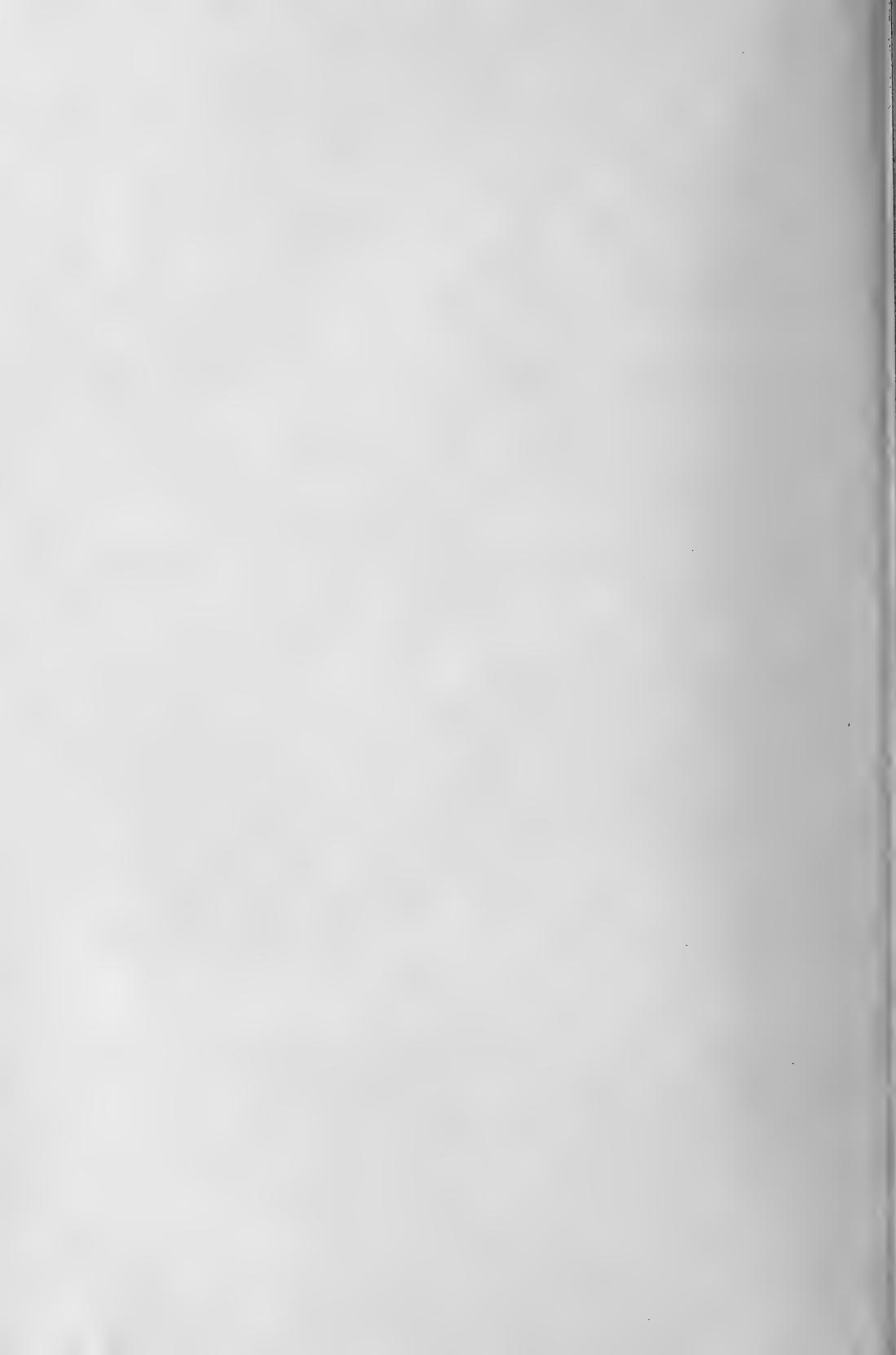
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M. A. LIEFTINCK. — Notes on the nomenclature and synonymy of Old World Melittine and Anthophorine bees (Hymenoptera, Anthophoridae), pp. 269—284, figs. 1—43.



# NOTES ON THE NOMENCLATURE AND SYNONYMY OF OLD WORLD MELECTINE AND ANTHOPHORINE BEES (HYMENOPTERA, ANTHOPHORIDAE)

by

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## ABSTRACT

*Tetralonoidella* Strand, 1914, is a forgotten name that has fallen into oblivion ever since it was defined and published. The name was given to an anthophorid bee of the Melectinae, which was described in some detail from Taiwan. As a validly proposed name it is resurrected, its monobasic type-species, *T. hoozana* Strand, 1914, being recognized as a distinct species, congeneric with, but differing specifically from, all described taxa formerly placed in *Protomelissa* Friese, 1914 (syn. nov.) or *Callomelecta* Cockerell, 1926. All ten presently known species are (re)defined, arranged in a key and, where necessary, illustrated by the author. Included are *T. nepalensis* spec. nov. (Nepal) and *fukienensis* spec. nov. (SE China), the latter being the first of its genus recorded from the Chinese continent. A redescription and figures are given of the little known holotype of *T. habropodae* (Cockerell, 1929), from Thailand, while the only known specimen of *T. iridescens* (Friese, 1914), from Taiwan, is probably lost but considered conspecific with *T. hoozana* Strand from the same island.

A second chapter deals mainly with six undoubtedly validly proposed specific names given by Newman (1835) to trivial variations of *Melecta albifrons* (Forster, 1771), collected in England. Two of these, *alecto* and *megaera*, were first described as new by Newman but quite accidentally proposed also by Lieftinck (1974), to denote two new species found in the Near East. These new homonyms are here replaced by *M. diligens* nom. nov. and *munda* nom. nov., respectively. — Lastly, in the anthophorine host bee genus *Habropoda* F. Smith, the unique type of *H. krishna* Bingham, 1909, proved to be conspecific with *H. apatelia* Lieftinck, 1974, the last-mentioned name thus being placed in the synonymy of *H. krishna* Bingham.

## *Tetralonoidella* STRAND, 1914, A PARASITIC ORIENTAL BEE GENUS RE-INSTATED

Since publication of my revision of the melectine genus *Protomelissa* Friese, 1914 (see Lieftinck, 1972: 267—282, figs. 1—16, pl. 1 figs. 1, 2, with map), some important nomenclatural changes on the genus and species level have again become necessary. As pointed out in that last paper, Friese's diagnosis of *Protomelissa* was published in June, 1914. Since the two Taiwanese melectines *Anthophora sauteri* Friese (original description published 15 May, 1911), and *Melecta formosana* Cockerell (the same dated March, 1911), turned out later to be conspecific, *formosana* became the type-species of *Protomelissa*. However, at that time it was still unknown that few months earlier (April—May, 1914), E. Strand had already published notes and a description of a very puzzling bee, like-

wise found in Taiwan (Formosa) which he "conditionally" named *Tetralonoidella*, with the monobasic type-species *T. hoozana* Strand. As we will see, the unique type of this bee is congeneric with both *Protomelissa* Friese and the much later described genus *Callomelecta* Cockerell, 1926 (type-species *C. pendleburyi* Cockerell, from the Malay Peninsula).

The original account of *Tetralonoidella hoozana* Strand was published in German and, for a better understanding of the situation, is here copied verbatim under that species. By the absence of a female, the unique male was mistaken for some non-parasitic, pollen-collecting member of the Eucerinae presumably related to *Tetralonia*. Unfortunately, this resulted in the choice of that whimsical generic (or subgeneric) name *Tetralonoidella* which is, of course, a veritable misnomer. It is not strictly a nomen oblitum since the whole description was simply

overlooked and forgotten ever after its introduction, no mention having been made of it in any catalogue or faunal list of the Apoidea. The reasons for this neglect are easily understood because (1) Strand's story of the affinities of *Tetralonioidella* is confused, the whole account being full of thoughts couched in deceptive terms leaving no room for conclusions; (2) one of the most outstanding characters of this bee, viz., the presence of a pair of robust mesoscutellar processes, was left unnoticed; and (3) Friese's almost simultaneously published definition of the genus *Protomelissa* was not known to Strand.

Considering the above facts, it will be clear that *Tetralonioidella*, though proposed conditionally, is the oldest available name amongst those of the included co-ordinate synonyms, i.e. *Protomelissa* and *Callomelecta*. Even if the provisions laid down in art. 33 (sect. b i and ii) of the law of priority in the Code, are taken into consideration, its validity and re-introduction cannot be called in question.

The synonymy, then, is briefly as follows:

#### *Tetralonioidella* Strand

*Tetralonioidella* Strand, April—May, 1914: 139—141  
(type-species: "*Tetralonia* (?) *hoozana*" Strand, 1914).

*Protomelissa* Friese, 1 June, 1914: 322, 323 (type-species: *Anthophora sauteri* Friese, May, 1911 = *Melecta formosana* Cockerell, Mar., 1911). — Sandhouse, 1943: 592 (type-species invalidly proposed: *Protomelissa iridescens* Friese, June, 1914 = *Tetralonioidella hoozana* Strand, April—May, 1914; *iridescens* syn. nov. — Liefstinck, 1972: 260, 261 (generic key), 267—270 (diagnostic char.) (type-species: *Melecta formosana* Cockerell, Mar., 1911).

*Callomelecta* Cockerell, 1926: 621 (type-species: *Callomelecta pendleburyi* Cockerell, 1926). — Liefstinck, 1944: 58—62 (gen. & spec. redefined); Liefstinck, 1972: 269, 270 (synon. notes).

The fullest account of the present genus is the one given by Liefstinck (1944, sub *Callomelecta*). It was based on a study of both sexes of three Malaysian species which on that occasion were elaborately described and keyed. These and other species were arranged also in the key published by me at a much later date (1972, sub *Protomelissa*). Except for specific differences in sculpture, body-colour, pubescent pattern and sexual structures, the above definitions of the male are fully applicable to the type-species *T. hoozana*, of which sufficient details can be

found in the next descriptive key and in Strand's original narrative copied thereafter.

#### KEY TO THE MALES OF *TETRALONIOIDELLA*

(N.B.—The ♂ of *T. tricolor*, and the ♀ of 5 other species are unknown)

1. Antenna long and slender, surpassing tegula; scape short, claviform, little curved, less than three times as long as diameter at apex; anterior face with conspicuous compact patch of longish, partly raised, silky and finely branched, pale yellow hairs pointing apicad. Segment 2 hairy, extremely short and annular, retracted and occasionally hidden from view (fig. 20); 3 also short but nearly thrice as long as 2, shiny and cup-shaped, only slightly shorter than its width at apex; 3—13 hairless or almost so, straight and cylindrical; 4—6 slender, 4 up to three times longer than its greatest diameter, 5—6 subequal but shorter than 4; remaining segments successively shorter toward end, more or less squarish, each with lateral carina, posterior faces rather flattened and increasingly more distinctly crenulated (fig. 13—14, 20). Thorax bulky, clothed densely with long fine plumose hairs. Abdominal tergites not banded, with short varicoloured pubescence. Inner rami of mid and hind tarsal claws distinctly shorter than outer, both acuminate and claw-like, not squarish or axe-shaped ..... 2
- Antenna shorter, not or barely surpassing tegula; scape long and slender, at least three times longer than broad, variably curved, often hairy but lacking conspicuous compact brush of finely branched silky hairs anteriorly; segment 2 often short and annular though not retracted and always plainly visible (figs. 10—12); 4—5 less markedly elongated, following segments relatively shorter than in next three species, not noticeably crenulated; last segment only little flattened below, not downcurved. Mandibles unidentate. Inner rami of mid and hind tarsal claws much shorter, squarish or axe-shaped (fig. 5) ..... 3
2. Integument of head, all thoracic sclerites and propodeum, deep black, only the face reddish black; ground colour of abdomen shining bright orange-rufous above and underneath, only the (partly retracted) tergites 4—6 on either side in front of graduli somewhat obscured, as is also the extreme

base of 7. Tergites not banded, almost bare, clothed sparsely with extremely minute appressed pale hairs; graduli at sides of 1, and 2 except upon middle, with narrow but slightly longer silvery yellow appressed hair-lines, also seen on about half of exposed portion of 4; hairs longer and sparser on disk of next tergites and on apical sternites, integument of the latter somewhat obscured upon middle at base. The following body parts are also light or dark ferruginous: glossal galea, mandible-bases, labrum, clypeus and antennae anteriorly, tegulae, and legs including coxae and trochanters. Antennal scape and flagellar segments posteriorly, brownish. Labrum relatively long: subequal to its width near base, anterior border broadly and deeply emarginate with well-rounded lobes (fig. 19). Mandibles simply sickle-shaped, lacking interior subapical tooth (figs. 17, 18). Tergite 7 shallowly excised, broadly V-shaped (fig. 21). Antennal segments (fig. 20) shaped much as in *himalayana* and *formosana*, the pale silky hair-patch covering front of scape conspicuous, flagellar segments less markedly crenulated but last joint distinctly swollen basally, then strongly hollowed out, downcurved and tapering to a point. Thorax posteriorly glossy reddish black; scutellum behind with median carina thickened at apex; spines long and slender, finger-like, directed straight back, feebly downbent, apices reddened, distinctly pointed, shorter than surrounding pubescence; metanotum and propodeum entirely smooth and polished. Inner rami of mid and hind tarsal claws but little shorter than outer. Thoracic pubescence uniformly pale-coloured, long and fluffy, hairs rather shorter and less closely set than in next two species. Thailand ..... *habropodae*  
 — Ground colour of abdomen less shiny, at least with basal portion of tergites 1—2 dark brown or black, clothed with short appressed tomentum differing in character: hairs either sparsely distributed, shortly branched, thin and darkest on exposed basal surface, or longer, more crowded together and distinctly plumose upon broad, paler-coloured apical margins of tergites; hence only basal part of 1—2 fully exposed and shiny, those of 3—7 withdrawn, leaving only dullish distal portions covered with closely set, dark golden-yellow plu-

- mose hairs. Mandibles with single interior subapical prominence. (For further details, see Lieftinck, 1972). Himalaya and Taiwan ..... *himalayana* and *formosana*
3. Pubescent colour-pattern of thorax and abdomen strongly contrasting, pile on thorax long, dense and feathery, fox-red to orange-rufous; and on abdominal tergites very short, scanty and mainly dark on glossy deep black ground, not concealing surface, tergites not or incompletely pale-banded. Three small to medium-sized closely similar species, all with labrum concave dorsally, strongly deeply punctate, the anterior border distinctly upturned ..... 6
- Pubescent colour-pattern of thorax and abdomen more uniform: pile on thorax dense though somewhat shorter and less bright, ochraceous-buff to ochraceous-orange; very short, less vivid and often forming complete, more or less definite hair-bands on dullish dark brown abdominal tergites ..... 4
4. Size rather large: body length ca. 13.5 mm; elongate, thorax and abdomen subequally broad, the latter gradually tapering, dull, lacking definite hair bands. Integument of abdominal tergites and sternites distinctly bicoloured: basal (i.e. narrowest) portion of 1—6 dark brown, the distal (postgradular and broader) parts of same semitransparent, distinctly paler, yellowish brown; all tergites with extremely short appressed hairs entirely concealing a finely superficially punctate surface, colour throughout ochraceous-buff to ochraceous-orange, hairs at bases of tergites 2—4 shortest and but little darker than on remaining parts. Labrum much shorter than broad, widest basally, apical border shallowly emarginate (fig. 4). Antenna relatively short, hardly reaching tegula; scape little curved, straight in dorsal view, 2 small but distinct, slightly broader than long, 3 and 4 elongate, distal flagellar segments only slightly crenulated (figs. 1—3). Metanotum finely wrinkled, base of propodeal triangle shiny though coarsely rugose for a distance equaling length of metanotum, triangle for the rest (save laterally) smooth and polished. Hind tarsal claw, fig. 5. Apex of tergite 7, fig. 6. Hidden sternites and genitalia, figs. 7—9. Dorsal thoracic pubescence relatively short but forming tufts of much longer hair surrounding, and practically concealing, the long curved scu-

- tellar spines. Taiwan ..... *hoozana*
- Generally smaller, body length 8.5—12.5 mm. Integument of abdominal tergites not noticeably bicoloured, i.e. uniform dark brownish black or black; tergal pubescence either short, decumbent and uneven, or forming more or less definite transverse pale subapical bands. Two very similar, probably nearly related species whose general appearance, texture and nature of pubescent pattern are almost identical ..... 5
5. Labrum short, broadest and more parallel-sided near base, and also shorter than in both *hoozana* (fig. 4) and *fukienensis*, mid-length to breadth ratio = 60.4 : 100, the emargination smaller and less deep than in *hoozana*, resembling *fukienensis* most closely (fig. 27). Antennal segments 3—4 subequally long, both relatively shorter than in *fukienensis* (fig. 12). Plate-shaped inner rami of mid and hind tarsal claws squarish, apices straight cut off. Apex of tergite 7 deeply broadly emarginate, the small prominent lobes rounded off (fig. 31). Mid-apical plate of sternite 7 parallel-sided (fig. 32). Dorsal thoracic pubescence xanthine-orange, hairs longer than in *fukienensis*; appressed tergal abdominal hair-bands 1—5(6) but little paler. Antennae and legs throughout dark reddish brown, tarsi becoming ferruginous distally. Body length 11.5—12.5 mm. For detailed descriptions of both sexes, see Lieftinck (1944: 71—75). West Java ..... *insidiosa*
- Labrum longer than in both *insidiosa* and *hoozana* (ratio = 75 : 100), greatest width slightly before midway length, sides more convex. Metanotum and propodeal triangle not very shiny, microscopically tessellate, extreme base of triangle distinctly wrinkled but lacking the strong ridges on either side of the median line seen in *insidiosa*; for the rest, propodeum, like *insidiosa*, more shiny and strongly punctate. Basal antennal segments, fig. 11. Plate-shaped inner rami of mid and hind tarsal claws axe-shaped, apices subacute: obliquely cut off. Apex of tergite 7 as in *insidiosa*, but emargination less wide and deeper, subrectangulate, the lobes more broadly rounded (fig. 28). Mid-apical plate of sternite 7 distinctly constricted basally, rather spatulate (fig. 29). Dorsal thoracic pubescence and tergal abdominal hair-bands as in *insidiosa* but all hairs shorter and paler, those covering ter-
- gites finer and more closely set. Antennae black above, dark reddish brown below; legs also darker than in *insidiosa*, the apical tarsal segments more reddish brown. Body length 11.5 mm, fore wing 8.5 mm. SE China ..... *fukienensis*
6. Labrum (fig. 22) not much broader than long, widest basally, slightly narrowing toward end, with outwardly convex sides, anterior border strongly upturned, more or less pinched in the median line, the apical emargination small and shallow in full dorsal view; surface shiny, strongly deeply punctate, punctures circular, smaller than interspaces. Antennal 4 slightly longer than 3 or 5 (fig. 10, ventral view) or subequal (dorsal view), and also differing from the next ones by having a dense coating of extremely minute, raised, silvery hairs; erect hairs on scape also longer than in next species. Scutellar spines finger-like, strongly downcurved, apex subacute or rounded, neither compressed nor bifid, surrounded by long fox-red pubescence. Metanotum finely wrinkled; propodeal triangle glossy black, throughout smooth and polished. Dorsal thoracic pubescence as in *pendleburyi*. Abdominal tergites 1 and most of 2 clothed sparsely with depressed plumose, pale orange-yellow hairs, those on 2 forming ill-defined postgradular bands not quite concealing surface; 3—4 similarly banded, subinterrupted by black. Apex of tergite 7 hairless, shaped as in fig. 23. Hidden sternites 7—8 and genital capsule, figs. 24 and 25—26, respectively. Size relatively small, total length 9.5 mm, fore wing 7.7 mm. Nepal ..... *nepalensis*
- Labrum distinctly broader than long, even more markedly so than in *hoozana* (fig. 4), anterior border either rather widely and deeply emarginate (*vulpecula*), or almost straight in dorsal view (*pendleburyi*). Antennal 3 and 4 subequal in length (figs. 15—16), raised hairs on scape and next segments all shorter and more sparsely distributed. Abdominal tergites deep black, 2—6 scarcely or not at all banded, the much shorter tomentum thin and more even ..... 7
7. Anterior border of labrum hardly upturned and almost straight in full dorsal view. Apical emargination of abdominal tergite 7 deeply U-shaped, subequal in form to the tubercles (Lieftinck, 1944, fig. 6), the punctuation similar to *nepalensis*. Scutellar spines



Fig. 1—9. *T. hoozana* Strand, ♂ structures, holotype Taiwan; fig. 1—3, basal segments of right antenna: fig. 1, lateral view of scape, long sparse raised hairs omitted; fig. 2—3, segm. 2—8, oblique ventral (2) and dorsal view (3); fig. 4, dorsal view of labrum; fig. 5, right hind tarsal claw, oblique inner view; fig. 6, apex of tergite 7, dorsal view, long bristly basal hairs mostly omitted; fig. 7—8, sternites 7 and 8, external view; fig. 9, genital capsule, ventral view of right half, scale line 1 mm.

robust, much shorter than in *nepalensis*, less downcurved, apex laterally compressed, distinctly bifid forming a pair of little knobs. Metanotum and propodeum dullish, finely tessellate, smooth, but much less shiny than in *nepalensis*, base of triangle coarsely punctate on either side, these sclerites separated from each other by a deep sulcus. Dorsal thoracic pubescence slightly paler than in *vulpecula*. Malay Peninsula .....  
..... *pendleburyi*  
— Anterior border of labrum abruptly upturned, the latter shaped much as in *nepalensis* but longer, emargination distinctly wider and deeper than in that species. Scutellar spines still shorter than in *pendleburyi*, directed obliquely caudad and but slightly downbent, apex somewhat compressed and tapering, slanting and bluntly pointed. Metanotum and propodeum much as in *pendleburyi*, but basal area of triangle coarsely longitudinally punctate along full breadth of same. Dorsal thoracic pubescence bright xanthine orange. Apex of abdominal tergite 7 with shallow impunctate median sulcus, otherwise black-haired, emargination shallower and wider than in both *nepalensis* (fig. 23) and *pendleburyi* (fig. 37). Sumatra ..... *vulpecula*

#### Tetralonioidella hoozana Strand (figs. 1—9)

*Tetralonioidella* ("*Tetralonia* (?) *hoozana* n.sp.") *hoozana* Strand, 1914 (April/May): 139—141 (♂ Formosa, Hoozan, ix.1910).

*Protomelissa iridescens* Friese, 1914 (1 June): 324 (♂ Formosa, Takao, Sept. 1908, H. Sauter). — Sandhouse, 1943: 592 (type-species of *Protomelissa*, not seen). — Lieftinck, 1972: 272 (key), 277, 278 (orig. descr. & notes; type not seen). *Syn. nov.*

Type material. — 1 ♂ (terminalia dissected out, glued on card and pinned on insect's pin), labelled: "Tetralonia (?) *hoozana* m. ♂ Strand det." (Strand's writing), "Hoozan Formosa H. Sauter x.10" (print, date written), "TYP JS" (typewritten on red), "Tetralonioidella *hoozana* Strand HOLOTYPE (= *Protomelissa iridescens* Friese), rev. MA Lieftinck 1979". Holotype ♂ in the former Deutsch. Entom. Institut (Eberswalde).

This is the first described and largest member of the genus. It fits the existing amended diagnoses of both *Callomelecta* and *Protomelissa* in all important characters and now becomes the type-species of the monobasic *Tetralonioidella*.

Male. — The uniform tint of the body pubescence is longest, tufted, and deepest orangish on the thoracic dorsum surrounding the practically invisible mesoscutellar processes, these long feathery hair-tufts being tipped with pale yellow. The neuration of the fore wing is much as in the drawing given for *T. pendleburyi* (see Lieftinck, 1972, fig. 11), i.e. the two proximal sides of the 2nd submarginal cell are subequal in length while the costal and anal sides of the latter are also about equally long though both are slightly less than half as long as the proximal sides.

The original description of *T. hoozana* is very full, as far as it goes, and is best copied along with the author's comments at full length, as follows.

#### "Gen. *Tetralonia* Spin.

*Tetralonia* (?) *hoozana* Strd. n.sp.

Ein ♂ von Hoozan IX.1910.

Dies Tier ist gewissermassen ein Mittelding zwischen *Tetralonia* und *Anthophora*. Eine *Anthophora* kann es aber nicht sein, weil die Ocellen in gerader oder fast gerader Reihe angeordnet sind (bei *Anthophora* bilden sie bekanntermassen ein ausgesprochenes Dreieck<sup>1)</sup>). Für ein *Tetralonia*-Männchen sind aber die Antennen eigentlich viel zu kurz; schon dadurch lässt die Art sich leicht von der sonst offenbar sehr ähnlichen *Tetr. himalayensis* Rad. unterscheiden. — Von *Ancyla* Lep. abweichend dadurch, dass die hinteren Metatarsen des ♂ kaum so lang wie die folgenden Tarsenglieder zusammen sowie nicht gekrümmmt sind, ferner ist der Clypeus vorstehend und die Körpergrösse ist bedeutender als bei den bisher bekannten *Ancyla*; soweit ohne Präparation erkennbar, sind die Mundteile ziemlich kurz. — Das zweite Geiszelglied ist kaum so lang wie das dritte und auch nicht dünner, das Tier somit, sowie durch die unter sich weit entfernten und subparallelen Augen von *Meliturga* Latr. leicht zu unterscheiden.

Es ist ganz wahrscheinlich, dass für dies Tier eine neue Gattung aufgestellt werden muss (die eventuell den Namen *Tetralonioidella* m. bekommen möge); um dies mit Sicherheit zu entscheiden, wäre aber die Kenntnis auch des ♀ eigentlich nötig. Aber auch wenn dies eine typische *Tetralonia* sein sollte, dürfte die neue Benennung als Untergattungsname verwendbar sein.

Schwarz; Mandibeln leicht gebräunt in der Mitte,

<sup>1)</sup> Anm. Die von Friese in: Verh. zool.bot.Ges. Wien 1911, p. 27, beschriebene *Anthophora* Sauteri n.sp. ist eher zu *Tetralonia* zu stellen, weil die Ocellen, wenigstens beim ♀, kein Dreieck bilden. In meiner Besprechung der Art im I. Teil dieser Arbeit (in: Suppl. Entomol. II, p. 51) habe ich leider unterlassen, dies Moment hervorzuheben.

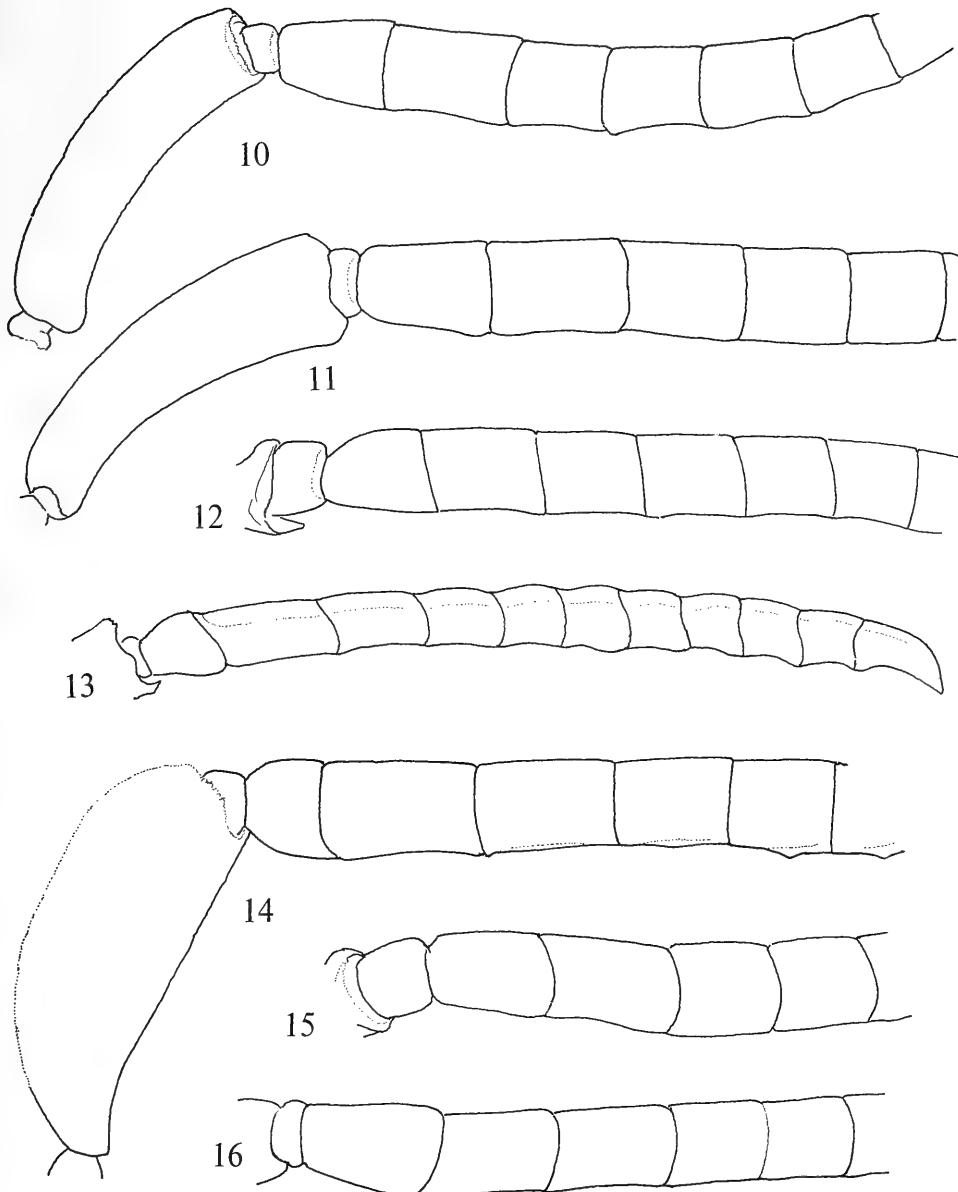


Fig. 10—16. *Tetralonioidella* species, partial view of right and left ♂ antennae; fig. 10, *T. nepalensis* spec. nov., Nepal, right segm. 1—8 showing plainly visible 2nd segment, long sparse hairs at scape omitted; fig. 11, *T. fukiensis* spec. nov., SE China, dorsal view of right segm. 1—7, same details; fig. 12, *T. insidiosa* (Lieft.), W. Java, right segm. 2—8, same scale; fig. 13—14, *T. himalayana* (Ckll.), Bhimtal, antero-ventral view of left segm. 2—13 and 1—7, lateral view, showing retracted 2nd segment (fig. 14 more enlarged, long silky hair-tuft at scape omitted); fig. 15, *T. vulpecula* (Lieft.), S. Sumatra, right antennal segm. 2—6, showing cup-shaped 2nd segment; fig. 16, *T. pendleburyi* (Ckll.), Larut Hills, Perak, the same of segm. 2—7 showing slightly shorter 2nd segment.

Labrum an der Basis beiderseits gerötet, Fühlergeiszel unten schwach gebräunt, Tegulae bräunlichgelb, der hintere Hälfte der Abdominalsegmente gerötet, die Tarsen leicht gebräunt. Flügel gleichmäßig schwach angerauht und etwas gelblich schimmernd, Geäder und Mal braunschwarz.

Der ganze Kopf hell graugelblich behaart und zwar auch auf dem Labrum lang abstehend, auf dem Clypeus ausserdem mit anliegender Behaarung. Thorax sehr dicht und lang ziemlich abstehend behaart und zwar auf dem Rücken orangefärblich, an den Seiten und unten heller behaart; die Skulptur daher nicht erkennbar. Rückensegmente des Abdomen mit feiner, kurzer, anliegender, nicht dichter, goldgelbener Behaarung, die auf der helleren Hinterhälfte der Segmente kaum heller als auf der basalen ist, als Gesamteindruck heben die helleren Binden sich daher wenig von der Grundfarbe ab. Die Bauchsegmente verhalten sich wie die Rückensegmente, jedoch ist ihre Behaarung in der Endhälfte leicht abstehend und die Segmente II und III zeigen ausserdem eine schmale helle Basalhaarbinde. Die Beine kurz und spärlich messiggelblich behaart.

Kopf schmäler als Thorax, aber breiter als lang, mit groszen, vorstehenden, subparallelen (nach unten ganz schwach konvergierenden), innen nicht ausgerandeten Augen und stark vorstehenden, vorn mitten jedoch abgeflachtem Clypeus, dessen Kontur, in Ansicht von der Scheitel, fast trapezförmig erscheint, im Profil scheint die Vorderfläche des Clypeus mit dem Labrum fast einen rechten Winkel zu bilden. Letzteres beiderseits an der Basis höckerig, am Vorderende (im Profil gesehen) leicht vorstehend. Die Antennen überragen die Mitte des Mesonotum, die Geiszel zylindrisch, nur das erste und die Basis des zweiten Gliedes etwas dünner als die übrigen; das zweite Geisselglied ist etwa dreimal so lang wie das erste. Abdomen erscheint in Draufsicht an der Basis breit quergeschnitten, am Ende zugespitzt, das letzte Tergit an der Spitze mitten leicht eingeschnitten. — Die dritte Kubitalzelle ist oben (vorn) so breit wie hinten, die zweite Kubitalquerader ist kurz unterhalb der Mitte stark saumwärts konvex gebogen, die zweite Kubitalzelle ist auf der Radialader nur halb so lang wie auf der Kubitalader. Körperlänge 13.5, Flügellänge 19 mm".

### *Protomelissa iridescens* Friese, — a dubious synonym?

For a discussion of this puzzling species, see the above citations, one of which includes a transcription of the original diagnosis. Expecting the type not to turn up any more in some European museum or private collection, it must be regarded as lost or destroyed. The locality labels and dates of capture of the types of *T. hoozana* and *iridescens* are quite different, so that the chances are very slight that Strand and Friese, at a time when both authors were studying bees from "Sauter's Formosa Ausbeute", did come across the same specimen and based their descriptions successively on this one individual. On the other hand, with the recent discovery of *T. hoozana*, one would be inclined to think *iridescens* and *hoozana* are identical species, because the probability of more than two taxa of this rare genus occurring together in such a small island as Taiwan, seems unlikely. Yet the obvious discrepancies in structure presently observed (table 1, especially points 3 and 4) in the types (if correctly stated for *iridescens*!), should not be neglected. Despite the incongruities I have, with all reserve, decided to synonymize these two Taiwanese species.

### *Tetralonioidella formosana* (Cockerell) comb. nov.

*Melecta formosana* Cockerell, 1911: 227, 228 (♀ Kosempo, Formosa).

*Anthophora sauteri* Friese, 1911: 127, 128 (♂ Tainan, Formosa).

*Protomelissa sauteri*; Friese, 1914: 323, 324 (♂ ♀ Tainan & Takao, Formosa).

*Protomelissa formosana*; Liefstinck, 1972: 273 (key); 274—277, figs. (♂ ♀ Kosempo, Tainan & Takao; orig. & further descr., synon. & full refs.).

Table 1. Differences in structure in the types of *T. iridescens* and *T. hoozana*.

<i>T. iridescens</i>	<i>T. hoozana</i>
1. Abdomen dull and with slight metallic sheen ("Abdomen mit Erzglanz", and "fast matt, schwach erzfarben schillernd");	1. Abdomen somewhat shiny but lacking any indication of metallic gloss
2. Labrum "viereckig, vorn schwach ausgerandet"	2. Labrum shaped as in fig. 4
3. Antenne rot . . . 2tes Geisselglied (segm. 3) viel kürzer als 3"	3. Antenna yellow-brown in front, dark brown behind, segm. 3 and 4 subequal in length (figs. 2, 3)
4. Apex of tergite 7 small and truncated ("klein und abgesetzt")	4. Apex of tergite 7 distinctly excised (fig. 6)
5. Body length 13 mm, width 4.5 mm	5. Body length 13.5 mm, width 4.5 mm

**Tetralonioidella himalayana** (Bingham) comb.

nov.

(figs. 13, 14)

*Melecta himalayana* Bingham, 1897: 516, fig. 172, insect, with left wing (♀ "Kumaon, 5000 ft., and probably throughout the Himalayas at and above that altitude".

*Protomelissa himalayana*; Lief tinck, 1972: 273 (key), 274, figs. 3, 7, 8 (addit. notes & ♂ struct., ♂ ♀ N & NE India).

Additional material. — Series of 12 ♂, NW India, U.P., Bhimtal near Nainital, 1500 m, 13, 14, 15 and 18.x.1978, M. A. Lief tinck, all at flowers of Labiate shrub *Plectranthus coetsa* Ham. ex D. Don. (local name "bhanira").

The above Bhimtal males are freshly emerged specimens in perfect condition. They were taken within a week's time, either in the early morning hours around 8.30 a.m., or on a return visit at 17 p.m. (4 on Oct. 14, 5 on Oct. 15, most of the remainder solitarily). All were attracted by flowers of the same plant, which grew in threes or fours at some distance from each other along a shaded forest path at the slope of a ravine. The bees flew in company with both sexes of 5 species of *Habropoda*, viz. *H. apostasia* m., *deiopaea* (Cameron), *hookeri* Cockerell, *pelmata* m., and *radoszkowskii* (Dalla Torre), the latter being by far the most common of these; females, besides taking nectar, assembled pollen at their hind tibiae and basitarsi, apparently also from *Plectranthus*. Their high-pitched notes could be heard already at about three yard's distance. I had asked Mr. Fred Smetacek, the owner of a small undisturbed patch of forest in the hills above Bhimtal, to keep an eye on the flowering season of *Plectranthus*, in 1979 and 1980. He kindly informed me in his letters that, unfortunately, no single inflorescence of plants could be found by him in any part of the same area during these next two years.

As pointed out by me earlier (1972: 273—277, sub *Protomelissa*), *himalayana* comes so close to *formosana* in stature, pubescent colour-pattern and other bisexual characters, that I have failed to discover more features than those already known for their separation. Nothing definite is known of their host relations, but both were associated in the field with *Habropoda* species, not with those of *Elaphropoda* as were other members of *Tetralonioidella*.

**Tetralonioidella tricolor** (Lief tinck) comb. nov.

*Protomelissa tricolor* Lief tinck, 1972: 273 (key), 278—

281. fig. 4 (labrum; ♀ Assam, Shillong; notes & host relations).

The ♀ holotype in the Berlin museum is still the only specimen so far known. By the absence of a ♂, nothing definite can yet be said about the nearest relatives of *tricolor*, but as stated in the original description, we may expect it to come closest to *himalayana* and *formosana*. The presence of a conspicuous dense brush-like patch of long hairs in front of the antennal scape of the ♂ (loc.cit.: 273), is a unisexual character, so that my subsequent remark (loc.cit.: 278) on its absence in the ♀ as a point of distinction between species-groups, is misleading.

**Tetralonioidella habropodae** (Cockerell) comb.

nov.

(figs. 17—21)

*Callomelecta habropodae* Cockerell, 1929: 133. — ♂ "Siam: Doi Sutep, on summit, Feb. 9, 1928 (Cockerell)". — Lief tinck, 1944: 62, 75, footnote (original material not seen).

*Protomelissa habropodae*; Lief tinck, 1972: 270 (key), 281 (orig. descr. copied, with notes; original material not seen).

Type material. — 1 ♂ (holotype), labelled: "Doi Setep Siam feb. 9 Alice Hacker" (?) in unknown writing; and "*Callomelecta habropodae* Ckll. TYPE", in T.D.A. Cockerell's hand; and, "acc. 35740" (AMNH label). Holotype in Amer. Mus. Nat. Hist., New York.

The more interesting characters of this remarkable little species are summarized in the preceding key. *T. habropodae* is known only from the unique holotype ♂. In addition to the key notes and the original description, copied in full on a previous occasion (Lief tinck, loc.cit. 1972: 281), most of the hitherto unnoticed peculiarities of structure are here also illustrated (figs. 17—21).

Apart from its smallish size and the predominantly orange-brown colour of the legs and abdomen, the species is easily distinguished from all allies by a combination of the following characters: dense brush-like hair-tuft in front of the antennal scape; characteristic shape of the mid and hind tarsal claws; the unarmed mandibles; and the superficially punctate shiny surface of the first two abdominal tergites. Disk of labrum (fig. 19) slightly concave, rather shiny, rugosely punctate, colour yellow-brown, its anterior border narrowly ferruginous, long hairs semi-erect, pale yellow, the border fringed with a

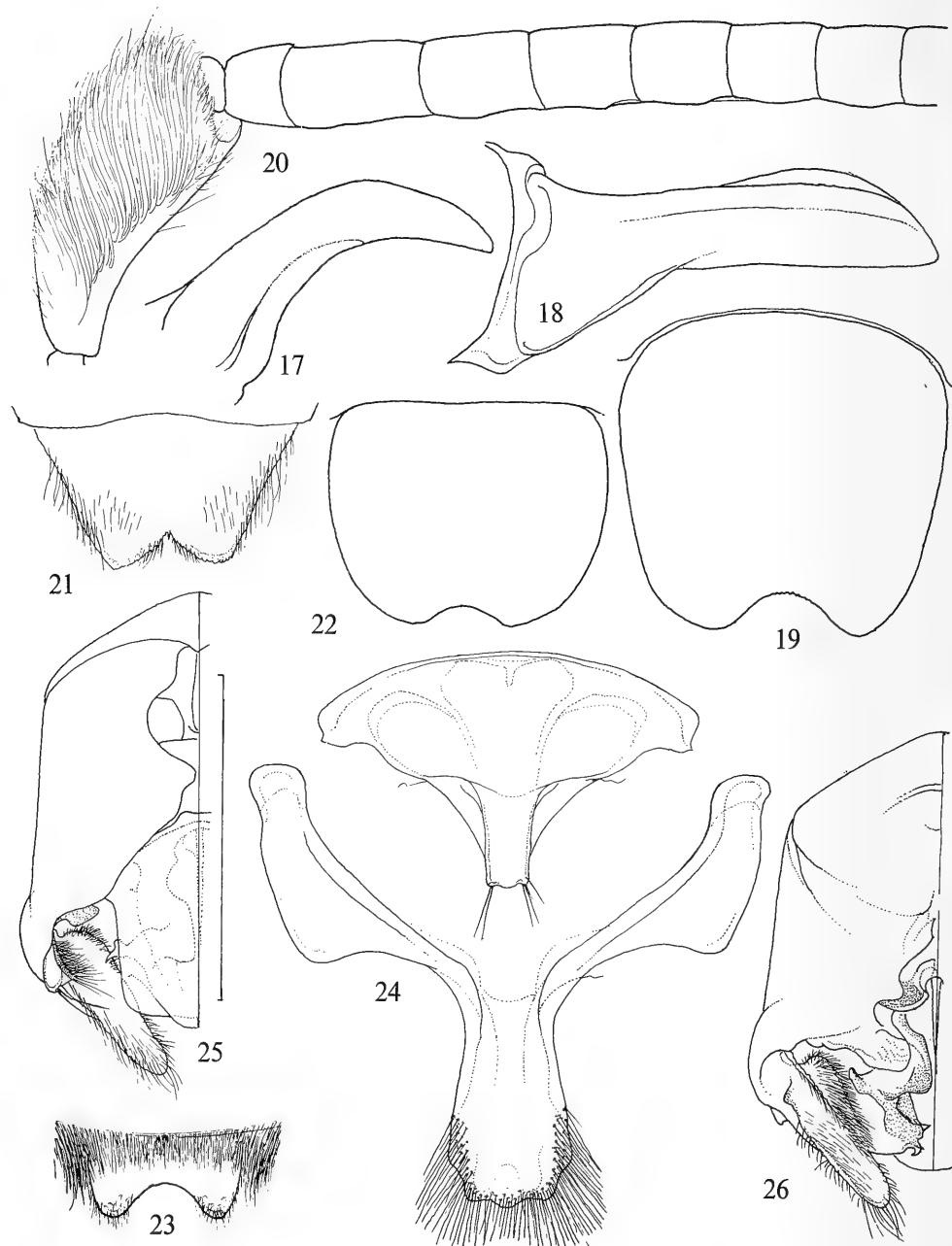


Fig. 17—21. *T. habropodae* (Ckll.), Thailand, ♂ holotype Doi Sutep; fig. 17—18, left mandible, inside and extero-lateral view; fig. 19, dorsal view of labrum; fig. 20, right antennal segm. 1—9, showing long silky hair-tuft at scape and partly retracted 2nd segment, inner (ventral) view; fig. 21, apex of tergite 7, dorsal view, most longish appressed hairs omitted. — Fig. 22—26. *T. nepalensis* spec. nov., ♂ holotype Nepal; fig. 22, dorsal view of labrum; fig. 23, apex of tergite 7, partly lacking bristly hairs; fig. 24, sternites 7 and 8, external view; fig. 25—26, genital capsule, dorsal and ventral view, scale line 1 mm.

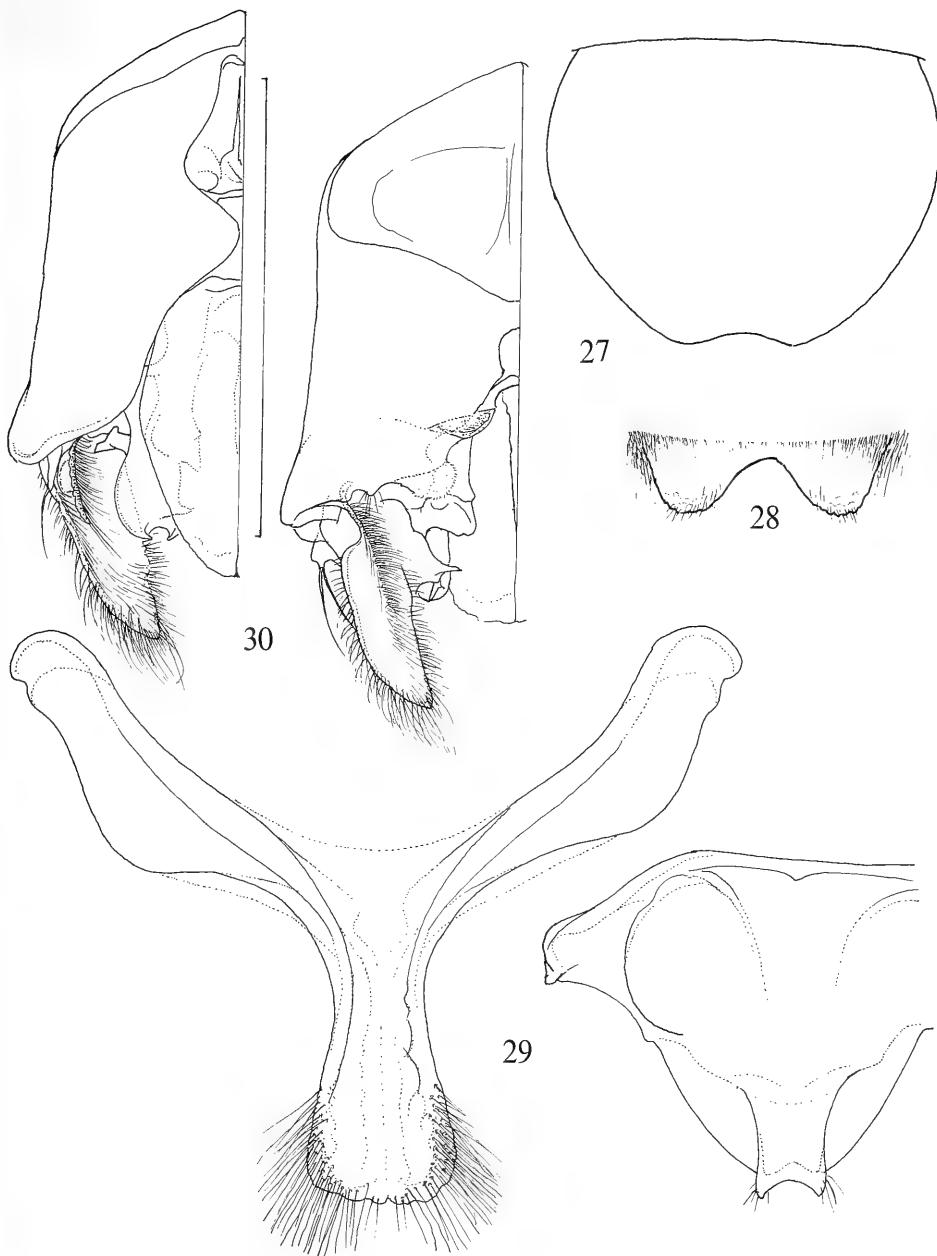


Fig. 27—30. *T. fukienensis* spec. nov., ♂ holotype SE China; fig. 27, dorsal view of labrum; fig. 28, apex of tergite 7, long depressed silky hairs mostly omitted; fig. 29, sternites 7 and 8, external view; fig. 30, genital capsule, dorsal and ventral view, scale line 1 mm.

row of stiff, parallel, pale golden bristles which are somewhat downcurved. Mandibles smooth, almost impunctate, pale brown, the apex obscured, almost black. Anterior rim of clypeus strong, ferruginous. The neuration of the strongly brownish amber-coloured fore wings is practically identical with that of *T. pendleburyi* (Lieftinck, 1944, fig. 1; and id., 1972, fig. 11). Abdominal tergite 7 (fig. 21) almost flat, surface densely rugoso-punctate, interspaces somewhat shiny, hairs pale, depressed. Body length 9.5 mm approx., fore wing 6.8 mm.

*T. habropodae* is undoubtedly most closely related to *himalayana* and *formosana*. It is of interest to note that in Thailand the species was found flying in company with its supposed host bee, *Habropoda sutepensis* Cockerell (for the latter, see Lieftinck, 1974: 198, 199, figs.). As we now know, *sutepensis* is a near ally of *H. apostasia* Lieft., which in N. India occurred together with *Tetralonoidella himalayana*.

#### *Tetralonoidella nepalensis* spec. nov.

(figs. 10, 22—26)

Type material. — 2 ♂ (terminalia of holotype dissected out, in pinned plastic capsule), E Himalayan Range, Nepal, Kathmandu, Godavari, 5000 ft., 6.viii. 1967, Canad. Nepal Exped. (holotype); and same loc., 6000 ft., 24 July 1967, same coll. (paratype). Holotype ♂ in Biosyst. Res. Inst., Ottawa (Ontario); paratype ♂ in Mus. Leiden.

Male. — Characters as given in the key and as shown in the figures.

This is the third of a small group of slender species characterized by a bicoloured pubescent body pattern: a long and dense fox-red vestiture covering the summit of head and all of the thoracic dorsum and sides, contrasting with an almost black unbanded abdomen. Differs from the Malaysian *pendleburyi* and *vulpecula* in the paler colour of the very short appressed hairs on parts of the abdominal tergites. In *vulpecula* these short hairs are almost black and evenly distributed, in the other two lighter and most marked at the postgradular lines, especially so in the present new species.

In the type the yellowish brown postgradular hairs on tergites 1—4 are broadest and longest at the sides of 1, more or less broadly interrupted by dark brown in the median line on tergites 2—4. The paratype differs from the type in that the pale hairs on 1 cover most of the surface and are evenly distributed, whereas on 2—4 they are

somewhat more crowded together, forming inconspicuous but uninterrupted bands. These complete bands are wholly absent also in *pendleburyi*.

#### *Tetralonoidella vulpecula* (Lieftinck) (figs. 15, 37—43)

*Callomelecta vulpecula* Lieftinck, 1944: 68—71 & 75—77, pl. & figs. (♂ ♀ Sumatra).

*Protomelissa vulpecula*; Lieftinck, 1972: 272 (key), 282, pl. 1 fig. 2 (♂ ♀ Sumatra, refs.).

No additional material.

#### *Tetralonoidella pendleburyi* (Cockerell) comb. nov. (fig. 16)

*Callomelecta pendleburyi* Cockerell, 1926: 621, 622 (♀ Malaya, Selangor). — Lieftinck, 1944: 62—68, figs. 1—9 & 75—77 (incl. keys ♀ ♂ and descr. allotype ♂, Perak and Pahang, Malaya).

*Protomelissa pendleburyi*; Lieftinck, 1972: (key), 282, figs. 9—16 (♂ ♀ Malaya, full refs.).

No fresh material. For structural details of the only known ♂ of this species, see Lieftinck, 1944 & 1972. On p. 62 line 17 in my 1944 paper, "♀ allotype" should be altered in "♂ allotype".

#### *Tetralonoidella fukienensis* spec. nov. (figs. 11, 27—30)

Type material. — 1 ♂ (terminalia dissected out, in pinned plastic capsule), SE China, NW Fukien, Chungan distr., Bohea Hills, 600 m, 25.ix.1939, T. C. Maa. Holotype ♂ in Mus. Leiden.

Male (slightly discoloured, but otherwise in fair condition). A species sufficiently characterized in the key. Superficially most closely resembling *T. insidiosa*, from West Java, but easily distinguished therefrom by comparing the structural illustrations here given for both. Differences not mentioned in the key are that *fukienensis*, besides being slightly larger in size, is decidedly a more robustly built species than *insidiosa*, especially the mid and hind femora and tibiae of *fukienensis* being markedly more swollen (expanded) about midway their length, than in the slenderer *insidiosa*.

#### *Tetralonoidella insidiosa* (Lieftinck) comb. nov.

(figs. 12, 31—36)

*Callomelecta insidiosa* Lieftinck, 1944: 71—75 & 75—77, pl. & figs. (♂ ♀ Java).

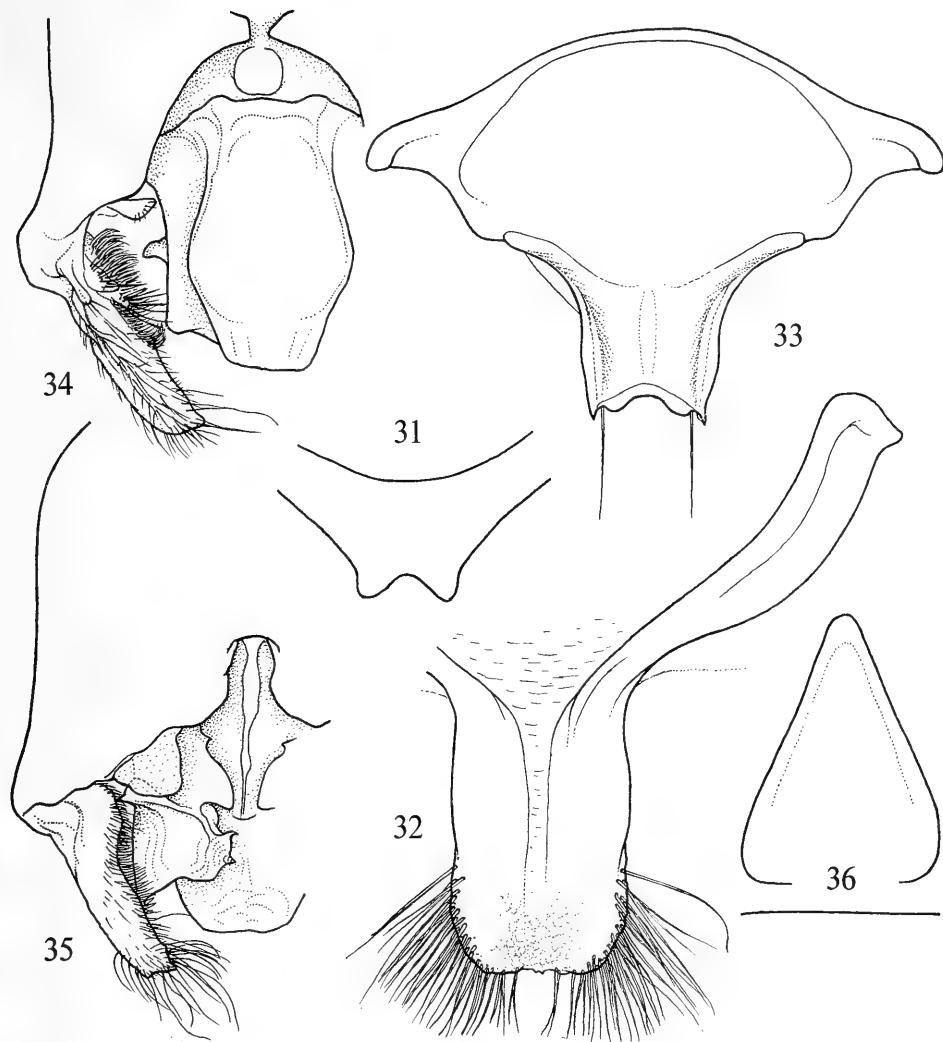


Fig. 31—36. *T. insidiosa* (Lieft.), ♂ and ♀ structures, W. Java; fig. 31, apex of ♂ tergite 7, ventral view; fig. 32—33, ♂ sternites 8 and 7, external view; fig. 34—35, ♂ genital capsule, partial dorsal and ventral view; fig. 36, ♀ pygidial plate, dorsal view (after Lieftinck, 1944).

*Protomelissa insidiosa*; Lieftinck, 1972: 272 (key), 282, pl. 1 fig. 1 (♂ ♀ Java, further notes).

No more recently collected material.

NEW NAMES AND SYNONYMS IN THE GENERA  
ELECTA ATREILLE 1802, AND HABROPODA F.  
SMITH, 1854

After publication of my "Prodrome" to a mo-

nograph of Palaearctic *Melecta* species (Lieftinck, 1980), Mr. D. B. Baker, of Ewell, indirectly brought to my notice that two specific names introduced in the *Prodrome* are preoccupied by those given to different taxa in the same genus by E. Newman, in 1835. As the last-mentioned names were followed by Latin diagnoses and descriptions in English, they are undoubtedly validly proposed and should take prece-

dence over those accidentally also chosen by myself. By an unfortunate oversight, Newman's introduction and diagnoses escaped my attention, while his names (extracted from Dalla Torre's catalogue) were inadvertently considered *nomina nuda* and therefore left out of consideration in my Prodrome. As a matter of fact, on pp. 513, 514 of his Entomological Notes (Newman, 1835), the author characterized six British "species" of *Melecta*, which he all named. Two of them were described as *M. alec-to* and *M. megaera*, both from localities in southern England and admittedly regarded by Newman himself as mere variants of the common *Melecta punctata* (Fabricius, 1775), a species now properly called *M. albifrons* (Forster, 1771)<sup>1)</sup>. The four remaining specimens of *Melecta*, all of them collected in England, were described in the same way to the former, receiving the names *M. atropos*, *clotho*, *lachesis*, and *tisiphone*. Although the validity of this nomenclature, like that of the other two, can not be called in question and should be borne in mind by future workers on the genus, they are of no concern in the present context.

<sup>1)</sup> In view of the many so-called "Spielarten" occurring in the entomological literature of the past, I am tempted to quote certain passages in Newman's cheerful introduction to the genus *Melecta* preceding the definition of his novelties, — contemplations which may give an idea of his and some contemporary authors' appraisal of specific names and the valuation of nomenclatural problems in general: — "It is pleasant to create a smile; and I anticipate that many smiles will be accorded me when I coolly assure your readers, that I am going to make six distinct species out of *Melecta punctata*, and that I cannot, for the life of me, tell to which of these the name *punctata* properly belongs, and therefore have given it to neither. It is pleasant to see one's new species given, without comment, as synonyms; and when this happens, and happen it certainly will to my *Melectae*, I hope I shall take it as good-humouredly as Mr. Waterhouse did, when he beheld his fourteen new *Notiophili* consigned to utter oblivion". "In these cases there is this comfort, that if the new-made species are really species, they will in the course of time be re-admitted: allow a year for each really new species parted from an old one; then the *Notiophili* will be re-admitted by the year 1847, and the *Melectae* — for I reckon them already struck out — by the year 1841".

Indeed, as time went on, re-adjustments in the nomenclature became almost prevailing topics of action, — though not always exactly in the way Edward Newman had predicted!

Summarizing the above, it will be clear that the two specific names *M. alec-to* Lief tinck and *megaera* Lief tinck, are preoccupied and should be substituted by new names, as follows:

*M. diligens* nom. nov. pro *M. alec-to* Lief tinck, 1980: 164, 186 (keys) & 273 (nom. preocc.). — Holotype ♂, Iraq, in Brit. Mus. (Nat. Hist.), London.

*M. mundula* nom. nov. pro *M. megaera* Lief tinck, op. cit.: 175, 185 (keys) & 243 (nom. preocc.). — Holotype ♂, Cyprus, in Mus. f. Naturk., Berlin DDR.

In the same work (1980), the following corrections should be made: p. 140 line 12, the wording "specific of varietal" should read "specific or varietal"; p. 290, line 11 from bottom, "figs. 231—232" should read "fig. 231"; p. 291, in the explanation of figs. 231—236, the word "antenna" should, of course, be replaced by "maxillary palpus", shown in fig. 232.

I shall gratefully accept any information about further errors and omissions occurring in this publication.

In the genus *Habropoda* F. Smith, the following case of synonymy could be established:

*Habropoda apatelia* Lief tinck, 1974: 171, 178 (keys), 215, 216, figs. ♂ ♀ Darjeeling, Syn. nov.

This taxon proves to be conspecific with the long-lost *H. krishna* Bingham, 1909 (Rec. Ind. Mus. 2: 366—367, ♂ Darjeeling 7000 ft.). Confirmed after direct comparison of morphology and internal structures of the well-preserved holotype of *krishna* (still in coll. Zool. Survey of India, Calcutta) with topotypical holotype of *apatelia* in the Brit. Mus. (Nat. Hist.) and paratypes in the Leiden Museum.

#### ACKNOWLEDGEMENTS

My best thanks are due to a number of entomologists who, through the years, kindly complied with my requests to recover certain melectine types and other valuable anthophorid specimens in various museum collections abroad. They kindly arranged for long-term loans to be made, and for waiting patiently for the ultimate return of specimens under their care: Messrs. H. Fankhänel (Leipzig, DDR), and G. Morge and J. Oehlke (both D.E.I., Eberswalde), for the loan of the long-concealed type of *Tetralonioidella* ? *hoozana* Strand. I am also grateful to J. G. Rozen Jr. (Amer. Mus. Nat. Hist., New

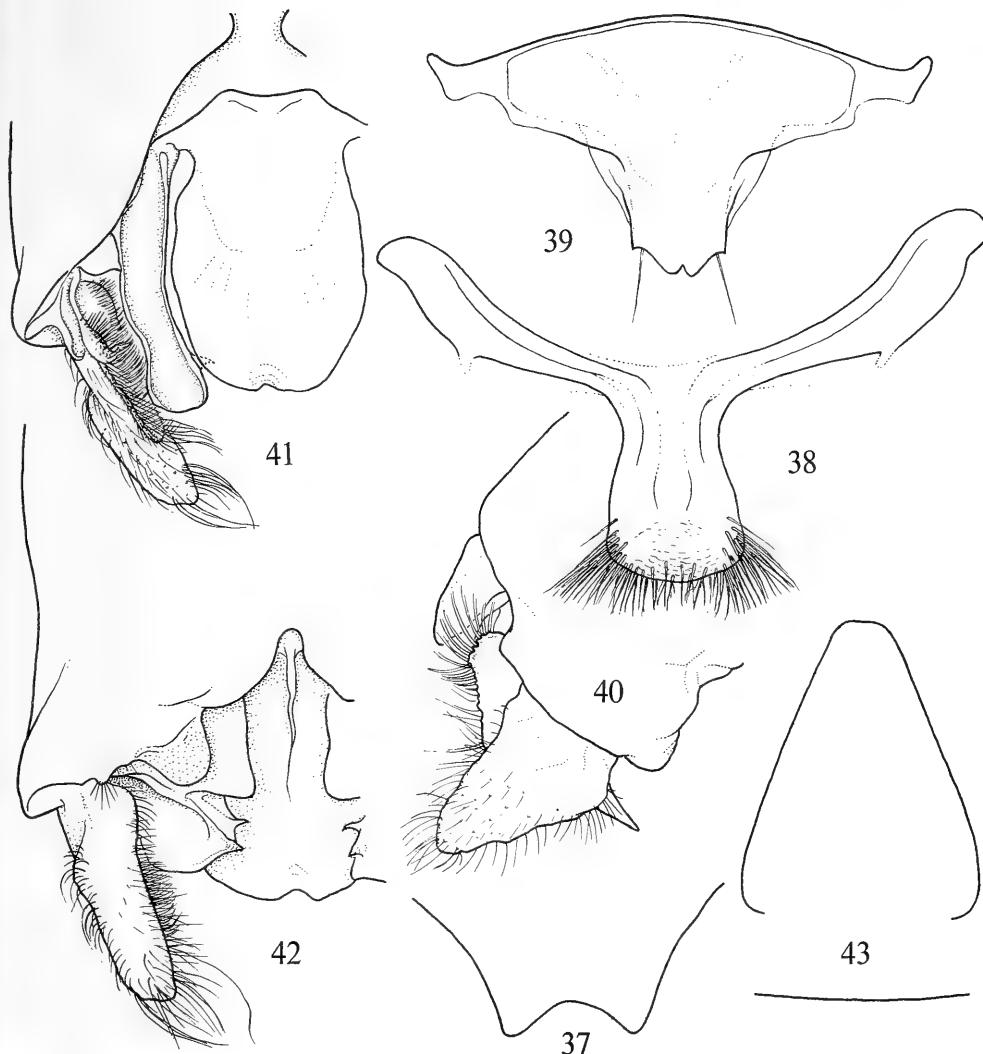


Fig. 37—43. *T. vulpecula* (Lieft.), ♂ and ♀ structures, S. Sumatra; fig. 37, apex of ♂ tergite 7, ventral view; fig. 38—39, ♂ sternites 7 and 8, external view ( $s_8$  slightly more downpressed); fig. 40, right lateral view of distal portion of genital capsule; fig. 41—42, apices of ♂ genital capsule, dorsal and ventral view; fig. 43, ♀ pygidial plate, dorsal view (after Lieftinck, 1944).

York) for the type loan of *Callomelecta habropoda* Ckll.; to J. R. Barron, J. E. R. Martin and W. R. M. Mason (Biol. Res. Sta., Ottawa, Ont.), for specimens collected by members of the Canadian Nepal Expedition 1967, which included the type of *Tetralonioidella nepalensis* spec. nov.; and to T. C. Maa (Taichung, Taiwan), for his great interest in the cuckoo bees of the present genus and their hosts, as well as for numer-

ous Anthophoridae assembled by him in Fukien during the first years of World War II, on which occasions the type of *T. fukienensis* spec. nov. was discovered. Lastly, I am indebted to L. B. Holthuis (Leiden), who found out the exact dates of issue of some articles, which appeared almost simultaneously in different European journals.

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## TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING

## REGISTER VAN DEEL 126

\* Een sterretje duidt aan een naam nieuw voor de wetenschap

\* An asterisk denotes a name new to science

Of the contribution by R. de Jong — Annotated list of the Hesperiidae of Surinam — of the names of species and subspecies only those of the taxa described as new are included.

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